The Contribution of Mortality to Early Coniferous Forest Development

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Abstract

The Contribution of Mortality to Early Coniferous Forest Development

James A. Lutz

Chair of the Supervisory Committee:
Research Professor Charles B. Halpern
College of Forest Resources

Tree mortality is a critical but understudied process in the development of young coniferous forests. Current successional models assume that mortality during the early stages of forest development is dominated by density dependent processes, but few long term studies exist to test this assumption. This study examines the temporal and spatial distribution of mortality and its causes over a 23-yr period in two experimental watersheds. A total of 193 permanent plots was sampled six times between 1979 and 2001 (14-38 yr after disturbance), generating 75,126 data records incorporating 7,146 mortalities. As a cause of mortality, suppression was observed in >80% of plots and was more than 2.5 times as common as mechanical damage (windthrow, stem snap, and crushing). However, biomass lost to mortality via mechanical damage was nearly four times that lost via suppression. Mechanical damage killed larger stems. Moreover, mechanical damage was episodic and spatially aggregated in the form of small to large windthrow patches. Rates of mortality varied greatly among species and with time. Overall rates of stem mortality were 1.0-5.3% per yr, whereas overall rates of biomass mortality were 0.4-1.7% per yr. Early seral hardwood species had rates of stem mortality as high as 9.7% per yr, but biomass increased with time as dominant stems achieved large sizes. *Cornus nuttallii* (Pacific dogwood) was the exception: it decreased in biomass primarily due to losses to *Discula destructiva* (dogwood anthracnose), an introduced pathogen. Shade-tolerant conifers, *Tsuga heterophylla* (western hemlock) and *Thuja plicata* (western redcedar), typically assumed to play a minor role in the development of young forests, accounted for 26% of stems 38 yr after disturbance. Although rates of suppression were low for this group, mortality due to mechanical causes (primarily crushing) exceeded that of other species. The choice of metric — proportion of stems or biomass lost — yields different conclusions about the relative importance of different forms of mortality. Although frequent in time and space, suppression leads to subtle changes in forest structure; the larger sizes and spatial aggregation of trees killed by mechanical causes yield greater ecological change by enhancing spatial heterogeneity of structure and composition. It thus appears that gap-forming processes that contribute to structural complexity in old growth can also be active in young forests.

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ACKNOWLEDGEMENTS

Any study using long term ecological data must credit those who originated the study, as well as those responsible for collecting and husbanding the data over many years. Jerry Franklin initiated this study of forest overstory development by expanding on the permanent vegetation plots originally established by Ted Dyrness. It was Jerry's hope that these tree plots would provide insight into forest successional processes for at least a century. The permanent sample plots are currently overseen by Charlie Halpern. Steve Acker, Richard Brainerd, Howard Bruner, Mark Klopsch and Gody Spycher contributed greatly to data collection and data integrity. Many others assisted with field measurements and data entry.

For this study, I would like to first and foremost acknowledge Charlie Halpern, my thesis advisor, for his kind guidance, intricate knowledge of forest ecosystems, and relentless dedication to quality. I would also like to acknowledge my advisory committee, Doug Sprugel and Don McKenzie, for their knowledge and support. Jerry Franklin and Steve Acker, whose previous work made this study and its conclusions possible, graciously provided their time, advice, assistance, and comments on this manuscript.

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DEDICATION

This thesis is dedicated to Masako, Eleanor and Emi.

INTRODUCTION

Tree mortality plays a critical, but often oversimplified, role in forest development. It can facilitate turnover in species composition (Shugart et al. 1981, Harmon et al. 1990, Runkle 2000), effect changes in forest structure (Franklin and Hemstrom 1981, Christensen and Peet 1981, Hibbs 1983), and alter rates of nutrient cycling or biomass accumulation (Marks and Bormann 1972, Marks 1974, Peet 1981, Harmon et al. 1990, Bormann et al. 1995). The demographic and ecological consequences of mortality can vary profoundly, depending on the context, physical scale, and causes of death. Catastrophic wildfires and hurricanes induce dramatic changes in forest structure and function, resetting succession at large spatial scales (Foster 1988b, Turner et al. 1997, Veblen et al. 1994, Sinton et al. 2000, Kulakowski and Veblen 2002). Gap forming disturbances result in smaller, but locally important changes (Runkle 1981, Stewart 1986, Canham 1989, Lertzman 1992, 1995, Busing 1995, Wright et al. 2003). In contrast to allogenic causes, gradual death of individual trees through physiological stress or competitive suppression may elicit only subtle responses of neighbors and little or no ecological effect.

In most forest ecosystems, detailed knowledge of the temporal and spatial distributions of mortality, its causes, and the ecosystem responses to mortality are limited by two practical considerations: the life spans of most tree species and the infrequent or episodic nature of death. Dendroecological methods can be used to reconstruct temporal and spatial patterns of mortality and associated growth responses (e.g., Taylor and Halpern 1991, Mast and Veblen 1994, Winter et al. 2002a). However, many forms of mortality can go undetected. Chronosequence studies can be used to characterize general trends in forest development (e.g., McArdle at al. 1949, Spies and Franklin 1991, Drake and Mueller-Dombois 1993), but can offer only limited insights into the rates, causes, and ecological consequences of tree mortality. Few approaches can provide the direct evidence afforded by long-term measurements of permanently tagged trees (Munger 1946, Harcombe 1986, Franklin 1989, Picket 1991, Condit 1998, Laurance et al. 2004).

In this study, I present 22 years of tree growth and mortality data from early successional forests dominated by Douglas-fir (*Pseudotsuga menziesii*) in two former old-growth watersheds in the western Cascade Range of Oregon. These data encompass a portion of the dynamic period of stand development known as "thinning" or "stem-exclusion" (Oliver 1981, Peet and Christensen 1987, Spies and Franklin 1996). Succession in these forests is typically portrayed as a relatively simple unidirectional process of growth and mortality (Oliver 1981, Peet 1981, Franklin et al. 2002). In forests dominated by *Pseudotsuga* this progression includes (i) an "establishment" period dominated by shrubs and shade-intolerant hardwoods, (ii) rapid growth of *Pseudotsuga* leading to closure of the canopy and loss of hardwoods, and (iii) intense intraspecific competition resulting in density-dependent mortality. It is generally assumed that hardwoods show limited persistence, that suppression is the dominant form of mortality, and that recruitment of shade-tolerant species does not occur until much later in succession (Oliver and Larson 1996, Franklin et al. 2002). This may be an overly simplistic model of both stand dynamics and mortality processes.

Although tree death is often the consequence of multiple factors or events (Manion 1981, Franklin et al. 1987, Waring 1987), distinguishing among causes that arise from distinct physical or biological processes allows us to examine the attendant ecological outcomes. These causes can vary among species with different life histories or canopy architectures (Foster 1988b, Acker et al. 1996, Lertzman et al. 1996, Canham et al. 2001, Acker et al. 2003), and can change in importance during succession (Bible 2001, Canham et al. 2001). Suppression mortality is assumed to occur in all forests in which densities are high enough to induce competition for resources. A significant body of work has been devoted to this process in single-species stands (Yoda et al. 1963, Mohler et al. 1978, Kenkel 1988, Pittman and Turnblom 2003) and to some extent, in species mixtures (Peet and Christensen 1989, Binkley 2003, Canham et al. 2004, D'Amato and Puettmann 2004, Deal et al. 2004). As a density-dependent process, suppression typically leads to more uniform spacing of trees (He and Duncan 2000, Gratzer and Rai 2004, North et al. 2004). Because species differ in their tolerance of shade, suppression can also lead to loss of diversity. However, because mortality is typically preceded by a gradual decline in vigor, the ecological effect of suppression can be subtle.

Pathogen- and insect-induced mortality can take many forms and affect forests at a variety of scales at various points in succession (Mueller-Dombois 1987, Hansen and Goheen 2000, Rizzo et al. 2000, Piri 2003, Filip and Ganio 2004). In coastal forests of the Pacific Northwest, insect-induced mortality is relatively uncommon (Childs and Shea 1967, Mason et al. 1998). However, root and stem rots are common, particularly in older forests (Childs and Shea 1967, Holah et al. 1997, Bible 2001, Ferguson et al. 2003) where they contribute to creation of snags, canopy gaps, and accumulations of wood on the forest floor.

Mortality induced by physical processes (e.g., windstorms, landslides, ice glazing, or snow loading) arises through infrequent, large-scale climatic events that create small to large patches of mechanically damaged trees (Lemon 1961, Stroempl 1971, Marks and Harcombe 1981, Rebertus et al. 1997, Sinton et al. 2000, Kramer et al. 2001, Hennon and McClellan 2003, Ryall and Smith 2005). Boles of larger stems are typically snapped or wind-thrown, and smaller stems are broken or crushed beneath them. This type of mortality produces sudden and often long-lasting changes in resource availability, microclimate, and forest floor conditions (Bormann et al. 1995, Van Pelt and Franklin 2000, Gray et al. 2002).

In this paper, I explore changes in the composition and structure of young coniferous forests in Pacific Northwest, how these are shaped by mortality and other processes, and what these changes imply for development of older forests. Considerable attention has been devoted to understanding the factors that contribute to structural complexity in old-growth forests in this region (Spies and

Franklin 1989, Tappeiner et al. 1997, Bible 2001, Kramer et al. 2001, Franklin et al. 2002, Poage and Tappeiner 2002, Winter et al. 2002a, b, Weisberg 2004). The results of the current study suggest that some of this complexity may arise through mortality and other processes early in stand development. My objectives are to: (1) quantify long-term changes in structure and composition in young coniferous forests, (2) interpret these changes through the demography of individual tree species, and (3) suggest how variation in the causes and spatial and temporal distributions of mortality contributes to the evolution of structure in older forests of the region.

STUDY AREA

Physical environment

Watersheds 1 and 3 (WS1 and 3) lie within the H. J. Andrews Experimental Forest (HJA; lat. 44°15’N, long. 122°12’W), 80 km east of Eugene, Oregon. As long-term experimental sites, they have a history of hydrological and ecological research that spans more than four decades (e.g., Rothacher et al. 1967, Dyrness 1969, Halpern 1988, 1989, Bond et al. 2002, Wemple and Jones 2002). The topography of these 100-ha basins is characteristic of much of the western Cascade Range, with steep dissected slopes separated by intermittent or perennial stream channels. Elevations range from 442 to 1082 m. Soils are primarily volcanic, originating from andesites, tuffs, breccias, and basalt flows (Rothacher et al. 1967). They range from shallow to moderately deep; textures are loamy and moderately stony, and porosity and water-storage capacity are generally high (Dyrness 1969).

The climate is maritime with mild, wet winters and warm, dry summers. Average minimum temperatures are -5.5°C in January and 11.9°C in August; average maxima are 5.5°C in January and 23.3°C in July (HJA primary meteorological station, 420 m). Annual precipitation is 2300 mm, but only 6% falls between June and August (Bierlmaier and McKee 1989); below 1000 m most of this falls as rain. Winter storms occur once or twice a decade and are characterized by wind and heavy precipitation (Read 2005).

Vegetation

WS1 and 3 lie within the *Tsuga heterophylla* zone (Franklin and Dyrness 1988). Prior to logging, forests were dominated by old-growth (300-500 yr old) and mature (125 yr old) *Pseudotsuga menziesii*, with *Tsuga heterophylla* and *Thuja plicata* of a variety of sizes and ages. Common sub-canopy species included the shade-tolerant conifer, *Taxus brevifolia* and the hardwoods, *Acer macrophyllum*, *Cornus nuttallii*, and *Castanopsis chrysophylla*. Six plant communities were defined prior to disturbance, reflecting a strong gradient in soil moisture availability. From “dry” to “moist” these were: *Corylus cornuta – Gaultheria shallon*, *Rhododendron macrophyllum – Gaultheria shallon, Acer circinatum – Gaultheria shallon, Acer circinatum – Berberis nervosa, Coptis laciniata,* and *Polystichum munitum* (Rothacher et al. 1967, Dyrness 1973). Nomenclature follows Hitchcock and Cronquist (1973).

History of disturbance

The timing of logging and broadcast burning differed between sites. The entire 96 ha of WS1 was clearcut over a 4-yr period (1962 -1966); logs were yarded with sky-line cables that required no road construction within the watershed. Slash was broadcast burned in October 1966. In WS3, three harvest units (5, 9, and 11 ha; 25% of the watershed) were cut over a single winter (1962-1963). A high-lead cable system was used to yard logs to three roads constructed within the watershed. Slash was broadcast burned in September 1963, thus initiating succession 3 yr earlier than in WS1. Reforestation also differed between sites. In WS1, *Pseudotsuga menziesii* was aerially seeded in October 1967 and 10 ha were reseeded in October 1968. Early establishment was generally poor and in April and May 1969, 2-yr-old *Pseudotsuga* were planted at 3-m spacing. Because of poor survival, 40 ha of the south-facing slope were replanted at 2.4 m spacing in April 1971. In WS3, 3-yr-old *Pseudotsuga* were planted between March and May 1964. Despite aerial seeding and planting, most *Pseudotsuga* regenerated through natural seeding (see *Discussion*).

METHODS

Sampling design and plot attributes

Circular plots of 250 m^2 were established in 1979 (WS3) and 1980 (WS1), 16 and 14 yr after broadcast burning. Plot centers coincided with the locations of permanent understory quadrats established in 1962, prior to harvest (Dyrness 1973, Halpern 1988, 1989). In WS1, 132 plots were spaced at 30.5-m intervals along six widely spaced transects oriented perpendicular to the main stream channel. In WS3, 61 plots were similarly spaced along two to four transects per harvest unit. Because the objective was to characterize development of upland forests, plots that fell in perennial stream channels were not established, nor were plots that fell on rock outcrops or on roads in WS3. Sample plots comprise ~4% of the harvested areas of the two watersheds.

Prior to logging, plots were assigned to one of the six plant communities and one of six soil types, reflecting parent material, depth, and profile development (Rothacher et al. 1967, Dyrness 1969). Plot locations were determined in 2004 using a differentially corrected Trimble GPS. Direct readings were made on 91 plots and the remaining locations were interpolated. I extrapolated elevation, aspect, and slope from GPS locations and a 10-m digital elevation model (Lienkaemper 2005). Mean annual insolation, considering both topographic shading and cloud cover, was extracted from earlier modeling work by Smith (2002).

Tree measurements

At plot establishment, all trees ≥1.4 m tall were identified by species and measured in one of three ways. For conifers larger than 2 cm diameter at breast height (dbh), a numbered tag was nailed at breast height (1.37 m), and diameter was measured at the nail. For smaller trees, a tag was loosely wired onto a branch and diameter was measured at the base of the tree (henceforth “dba stems”). Hardwood species often exhibited prolific basal sprouting, forming dense clumps (“clump stems”). For each clump, stems >5 cm dbh were tagged (or if all stems were < 5 cm dbh, the largest stem was tagged) and the remaining stems were tallied in two dbh classes (0.1-3.0 and 3.1-4.9 cm). Because it was not always possible to distinguish genets, I do not track the dynamics of individual clumps. All tagged stems were rated for vigor: 1 = good; 2 = fair (significant loss or discoloration of foliage or physical damage); 3 = poor (little foliage, mortality imminent). Additional descriptive notes were taken for stems with fair or poor vigor.

Remeasurements and assessments of mortality were made in 1984, 1988, 1991, 1995, and 2001. At each remeasurement, tags on dba stems were moved to breast height, if possible, and measurements were taken at both heights. Previously tallied clump stems were tagged and measured if large enough. “Ingrowth” stems (<1.4 m tall at the last measurement) were tagged and measured or tallied, as appropriate. A tagged stem that died since the last observation was measured for diameter, and the likely cause of mortality was recorded (see below). Occasionally, a tagged stem was not found; a stem missing for two sampling intervals was assumed to have died during the first interval. Diameter was then assumed to be that of the last measurement and cause of mortality was inferred from evidence of disturbance (e.g., adjacent windthrow or slope failure) or previous comments; otherwise, mortality was recorded as “unknown.”

It is often difficult to definitively assign cause(s) of mortality in trees because multiple factors often contribute to death (Manion 1991, Franklin et al. 1987, Waring 1987). However, it is possible to describe conditions at the time of mortality and thus to make reasonable inferences about cause. Using a classification system employed in other long-term studies of western forests (Bible 2001, Pincheira 2004, van Mantgem et al. 2004), field crews noted causes of mortality. I then consolidated these field characterizations into categories that reflect distinct physical or biological processes. Six general forms of mortality were considered:

(1) Suppression – smaller stems in subordinate canopy positions that exhibited slow growth, but no sign of physical damage or pathogen activity.

(2) Mechanical damage (resulting from wind or snow loading) – stems that were completely uprooted or whose boles were snapped or crushed beneath uprooted or broken stems.

(3) Crushed beneath old-growth trees – in two instances, old-growth trees fell into harvest units from adjacent forest.

(4) Slope failure – uprooted stems associated with local slope failure.

(5) Pathogens – two types of fungal pathogens were observed: (i) native root rots in *Pseudotsuga*. Symptoms included gradual loss or chlorosis of needles, absence of physical damage to boles or bark, and mortality often clumped in disease centers. Field crews did not distinguish among fungal species, but I revisited several infection centers in 2004 and verified presence of *Armillaria ostoyae*, a native pathogen. (ii) Dogwood anthracnose (*Discula destructiva*), an introduced fungal pathogen in *Cornus nuttallii*. Symptoms included distinctive brown spotting or senescence of leaves, with eventual dieback of twigs and entire stems. In addition to fungal pathogens, two instances of mortality attributed to hemlock dwarf mistletoe *(Arceuthobium tsugense*) were assigned to this category.

(6) Animal damage – stems that exhibited obvious signs of browsing damage or stripping of bark and cambium.

If sufficient evidence did not exist to assign a cause, mortality was recorded as "unknown" (26% of cases).

Data reduction and analysis

Plot-level summaries were computed for each species at each sampling date or measurement interval (for rates of change). Summary statistics were generated for both live and dead stems on a slope-corrected basis, and included estimates of density, basal area, and bole biomass, from which net primary productivity of boles (NPPB) was calculated, expressed on an annual basis:

$$NPPB = \Delta B + M \qquad [1]$$

where ΔB is the difference in live bole biomass between measurements and M is bole biomass of stems that died since the last measurement (Acker et al. 2002).

For basal area estimates, clump stems were assigned diameter-class midpoints (1.5 or 4.0 cm). For dba stems, dbh was estimated from species-specific regression equations developed from stems that had been measured at both heights. For each species, separate dbh-dba models were considered for WS1 and 3, but only for *Pseudotsuga* did the regression slopes differ significantly. Of a total of 14 species, four were too uncommon to warrant summary statistics; they were, however, included in plot totals. Trends in bole biomass paralleled those of basal area, thus for most analyses, only biomass is presented.

To estimate bole biomass, I followed the methods of Acker et al. (2002). Three general approaches were used (see Appendix II for details). For *Alnus rubra, Cornus nuttallii, Populus trichocarpa*, *Prunus emarginata,* and *Rhamnus purshiana*, bole biomass was estimated directly from dbh using regional equations in Means et al. (1994). For *Acer macrophyllum, Arbutus menziesii*, and *Castanopsis chrysophylla*, bole biomass was derived from volume equations based on dbh and height (Means et al. 1994), with heights estimated from dbh-height models of Garman et al. (1995). Standard values for wood density (M. Harmon, *personal communication*) were used to convert volume to mass (bark volume was assumed to be negligible for these species). For *Pseudotsuga menziesii, Thuja plicata*, *and Tsuga heterophylla*, wood biomass was estimated using dbh-volume equations (S. Acker, *unpublished data*) modified from those of Browne (1962). Bark volume was estimated from species-specific bark-to-wood volume ratios (S. Acker, *unpublished data*) and standard values for bark and wood density were used to convert volume to mass. For species lacking predictive equations, I substituted those of species with comparable growth form: *Pseudotsuga menziesii* for *Abies amabilis*; *Tsuga heterophylla* for *Taxus brevifolia* and *Calocedrus decurrens*; and *Alnus rubra* for *Cornus nuttallii*, *Prunus emarginata*, and *Rhamnus purshiana*.

To estimate rates of mortality among species and to partition mortality by cause, data were combined from both watersheds. Mortality rates were computed for each measurement interval, expressed on an annual basis (Sheil et al. 1995):

$$m = 100\ (1 - (N_t / N_o)^{1/t}) \qquad [2]$$

where m is mortality rate (percentage of stems per year), N_0 is the number of stems alive at the previous measurement, N_t is the number of stems from the previous measurement alive at the current measurement, and t is the number of years between measurements. For hardwood species, mortality rates represent underestimate: because smaller (<5 cm dbh) clump stems were not tagged, it was not possible to distinguish between stem survival and stem turnover (mortality and ingrowth). Mortality of these tallied stems was assumed only if the number of stems within a diameter class decreased between measurements (after considering the potential to advance to the larger class or to tagged status). However, if the number of stems within a class remained constant or increased, I assumed no mortality.

Regression trees (Breiman et al. 1984) were used to identify the environmental and biotic variables correlated with the two primary forms of mortality, suppression and mechanical damage. This method uses binary, recursive partitioning to split data into increasingly homogeneous subsets (McKenzie et al. 2000). For each plot, I summed the density of stems lost to suppression mortality and mechanical mortality over the study period; these cumulative mortalities served as response variables. A regression-tree model was then run for each response variable. The potential predictor variables were: (i) geographic and topographic variables: watershed, elevation, slope, aspect (“northeastness”; cos [aspect-45°]), closest perpendicular distance to forest edge, and closest perpendicular distance to southern ridgeline; (ii) insolation (MJ m^{-2} day^{-1}) from (Smith 2002); (iii) soil type (reflecting differences in depth and water retention); (iv) plant community (a surrogate for site productivity) and (v) two biotic variables: density of live stems and bole biomass at the first measurement (1979/1980), to test the hypothesis that stem density would correlate strongly with suppression-induced mortality. The regression trees were "pruned" using minimum-complexity criteria to eliminate branches that did not contribute significantly to reductions in deviance (Breiman et al. 1984).

RESULTS

Watershed-scale changes in forest structure and composition

Forest structure and composition changed markedly in both watersheds over the period of observation. Mean densities peaked at >3000 stems ha^{-1} 22-25 yr after disturbance, then declined rapidly (Fig. 1a). At final sampling (35-38 yr) densities were comparable to those at initial measurement. Mean basal area and bole biomass increased continuously, following nearly identical trajectories in the two watersheds (Figs. 1b, c). Net primary productivity of boles peaked earlier than biomass (30-35 yr; Fig. 1d), reflecting a large increase in mortality during the last measurement interval (see below).

Of 14 tree species observed, seven accounted for >97% of all stems and >96% of total biomass at each sampling date. *Pseudotsuga menziesii* was the dominant species, accounting for 50-58% of stems and 57-82% of biomass (Fig. 2a, b).

Densities of the four hardwood species peaked early – *Cornus nuttallii* and *Acer macrophyllum* at 18-21 yr and *Castanopsis chrysophylla* and *Prunus emarginata* at 22-25 yr (Fig. 2a). Densities of the two shade-tolerant conifers, *Tsuga heterophylla* and *Thuja plicata*, peaked later (29-32 yr), but declined during the last measurement interval. Nonetheless, at 35-38 yr, *Tsuga* accounted for 21% of stems (Fig. 2a).

Despite declines in density, most species showed continuous increases in bole biomass, albeit at varying rates (Fig. 2b). Of the subordinate species, *Tsuga* showed the most rapid accumulation of biomass, contributing 6% of total bole biomass at 35-38 yr. Among the hardwoods, *Acer* exhibited the highest rate of increase. *Prunus emarginata*, the only non-sprouting species, showed little change in biomass 29-32 yr after disturbance. *Cornus nuttallii* was the only species that exhibited a decline in biomass during the sampling period.

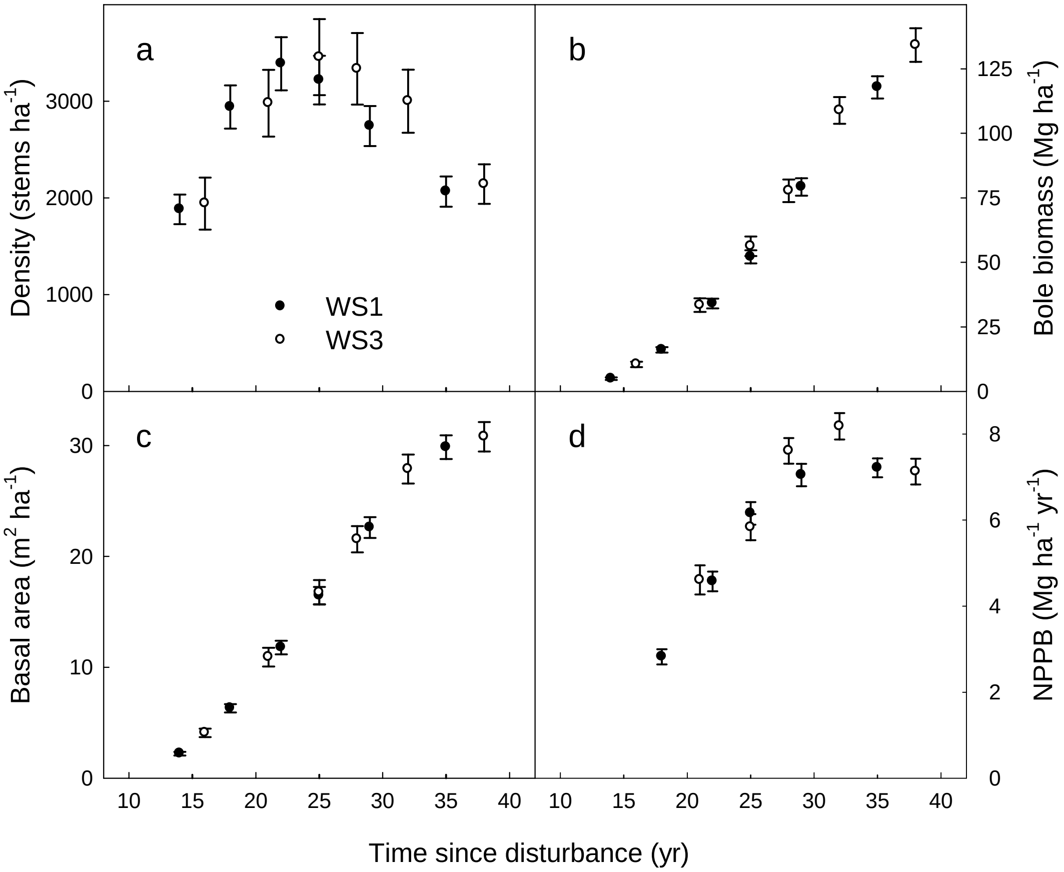

FIG. 1. Temporal trends in (a) stem density, (b) bole biomass, (c) basal area, and (d) net primary productivity of boles. Means ±1 SE are shown. Due to the different dates of cutting and broadcast burning, measurement years corresponded to different time since disturbance for each watershed.

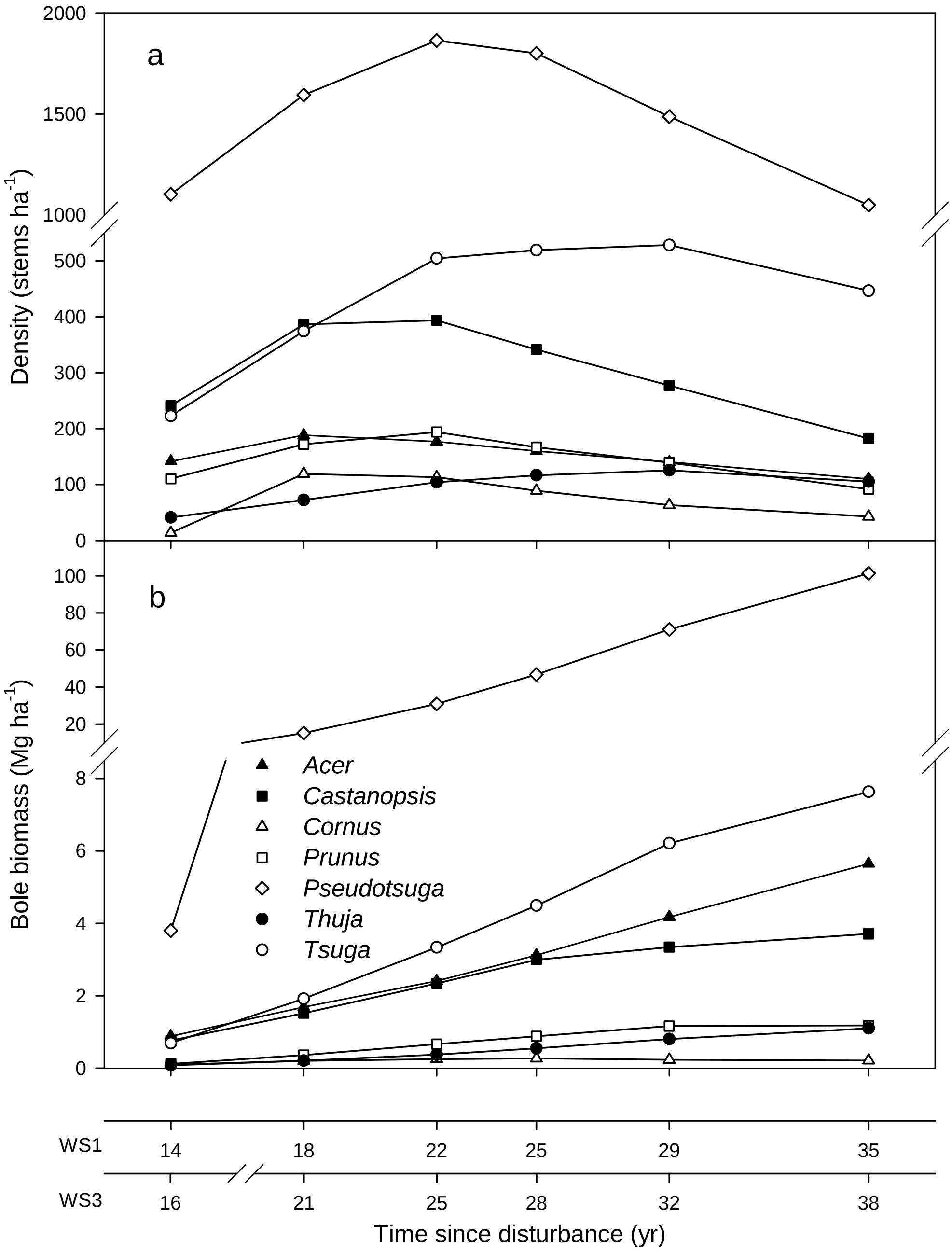

FIG. 2. Temporal trends in (a) stem density and (b) bole biomass for the seven common tree species. Data from both watersheds combined with points representing 2-3 yr intervals of time since disturbance. Secondary axes represent time since disturbance for each watershed.

Plot-scale variation in forest structure and composition

Both watersheds showed a large range of variation in stem density and bole biomass among sample plots (Fig. 3). Even with the more extreme values excluded, density at final sampling varied by two orders of magnitude and bole biomass by a factor of ten. Similarly, the contributions of hardwoods and shade-tolerant conifers to total density and biomass varied markedly among plots and through time (Fig. 4). Between the first and last measurements, the proportion of plots dominated by hardwoods (typically on south-facing slopes and shallower soils) decreased somewhat for density (29 to 21%) and more so for biomass (32 to 6%). In contrast, the proportion of plots dominated by shade-tolerant conifers tripled for density (6 to 17%), but changed little for biomass (7% for both measurements).

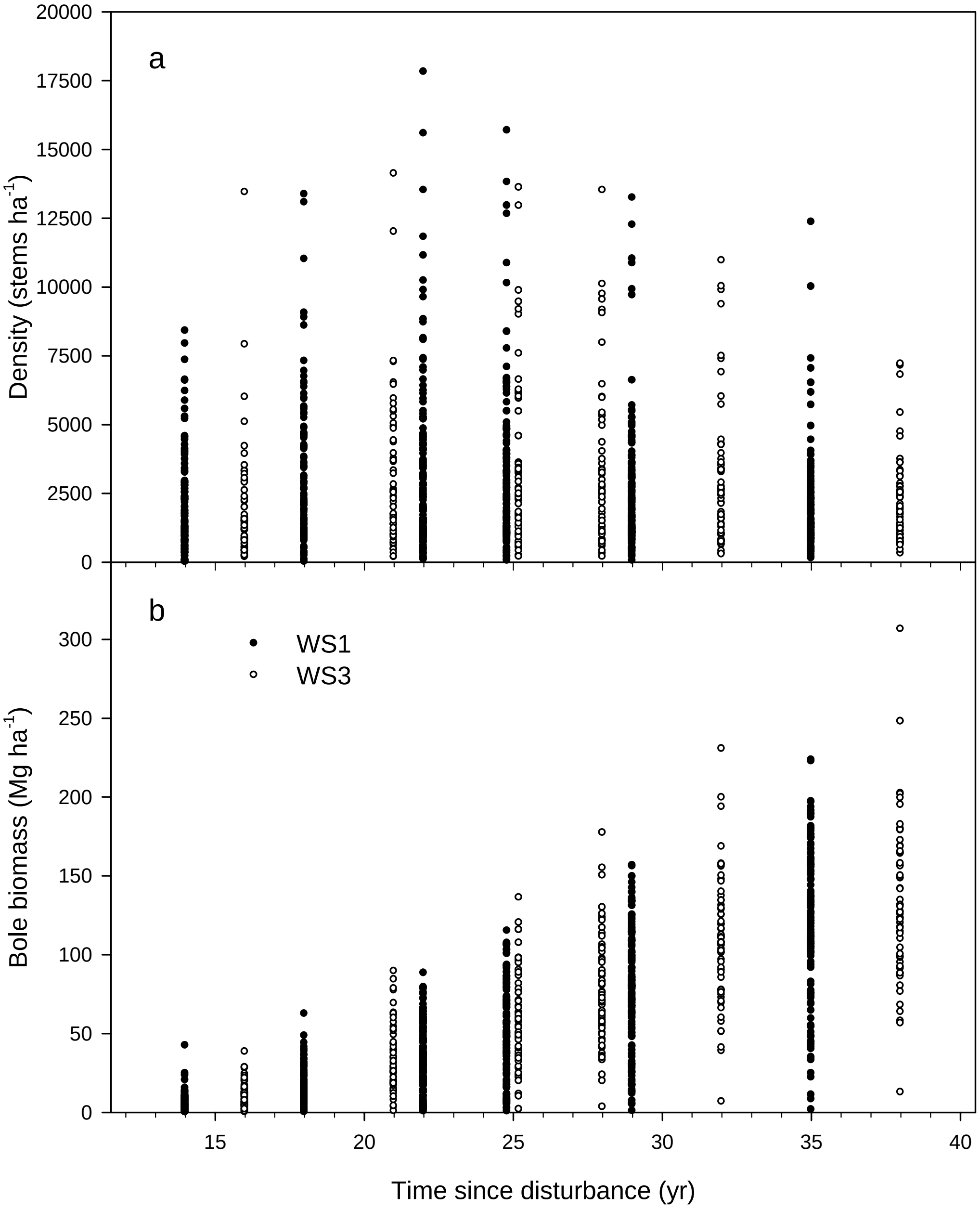

FIG. 3. Plot-level variation in (a) stem density and (b) bole biomass during each measurement year. Means and standard errors shown in Fig. 1a, b.

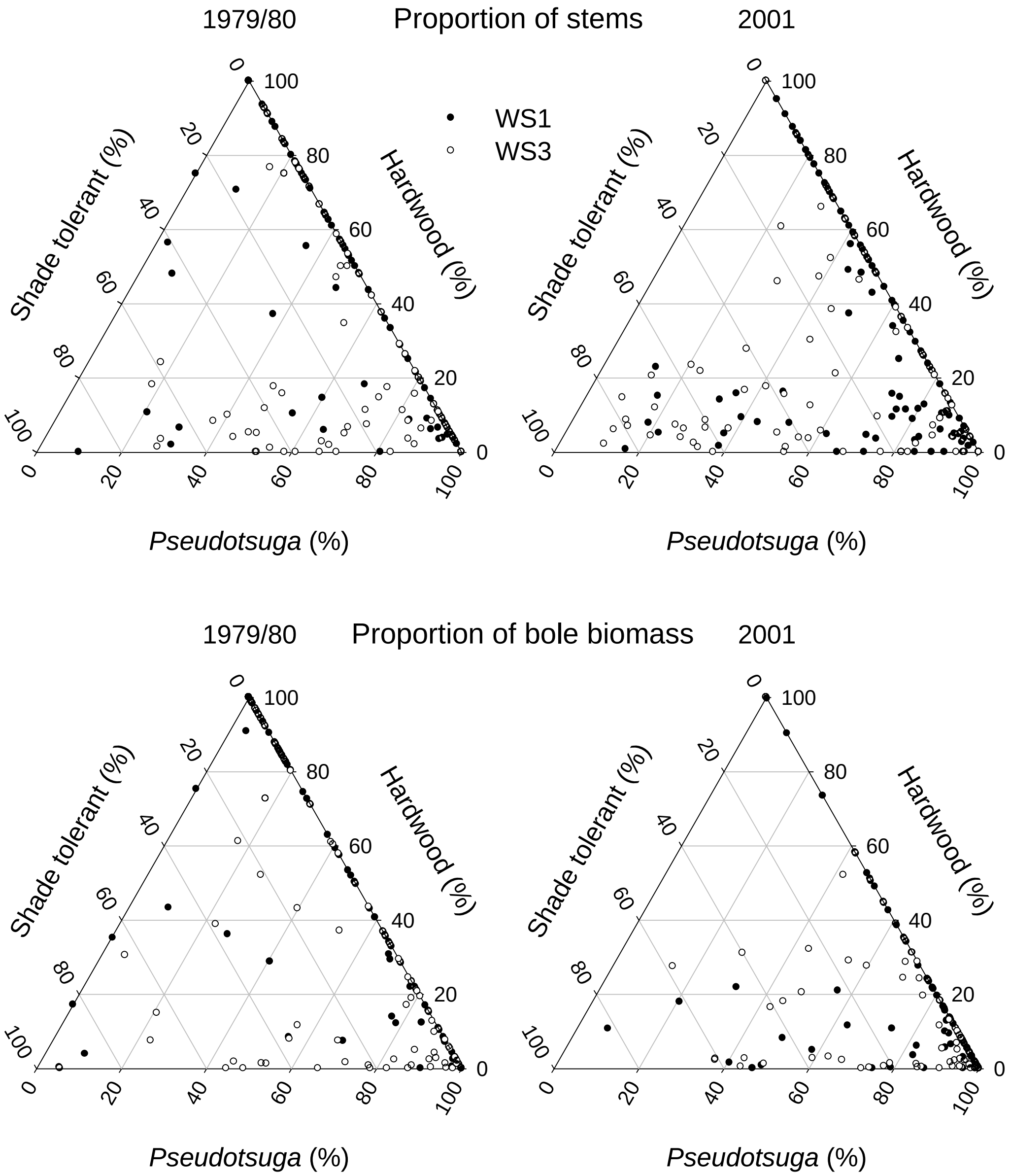

FIG. 4. Relative abundance (proportion of total) of *Pseudotsuga*, hardwoods, and shade-tolerant conifers in each plot at the first (1979/80) and last (2001) measurements. Proportions are based on the total number of stems (top) and bole biomass (bottom).

Temporal trends in mortality

Annual mortality rates increased over time from 1.0 to 5.3% of stems (Fig. 5a). As a percentage of total bole biomass, however, rates were low (<0.6%) and fairly constant until the last measurement interval (1.7%; Fig. 5b). All species showed proportionally greater mortality in numbers than in biomass (Figs. 5a, b), reflecting greater mortality of smaller diameter stems. In fact, rates for hardwood species may be considerably higher because of the conservative approach to estimating loss of small clump stems (see *Methods: Data reduction and analysis*).

Among species, three trends were observed. Hardwoods showed steep increases in mortality, peaking between 18 and 25 yr after disturbance (Fig. 5a). The highest rates were observed for *Cornus* (exceeding 9.6% over a 7-yr period), and the lowest for *Acer* (maximum of 5.4%). Mortality of *Pseudotsuga* increased more slowly, exceeding 5% after 25-28 yr. Shade-tolerant conifers (*Tsuga* and *Thuja*) exhibited consistently low mortality until the last measurement interval (29-38 yr) when rates increased to ~4%.

Trends in mortality expressed as a percentage of biomass were generally similar among most species. *Cornus* and *Prunus*, however, exhibited distinctly greater proportional loss of biomass than other species (Fig. 5b), reflecting a combination of higher rates of stem loss and greater losses of larger diameter stems.

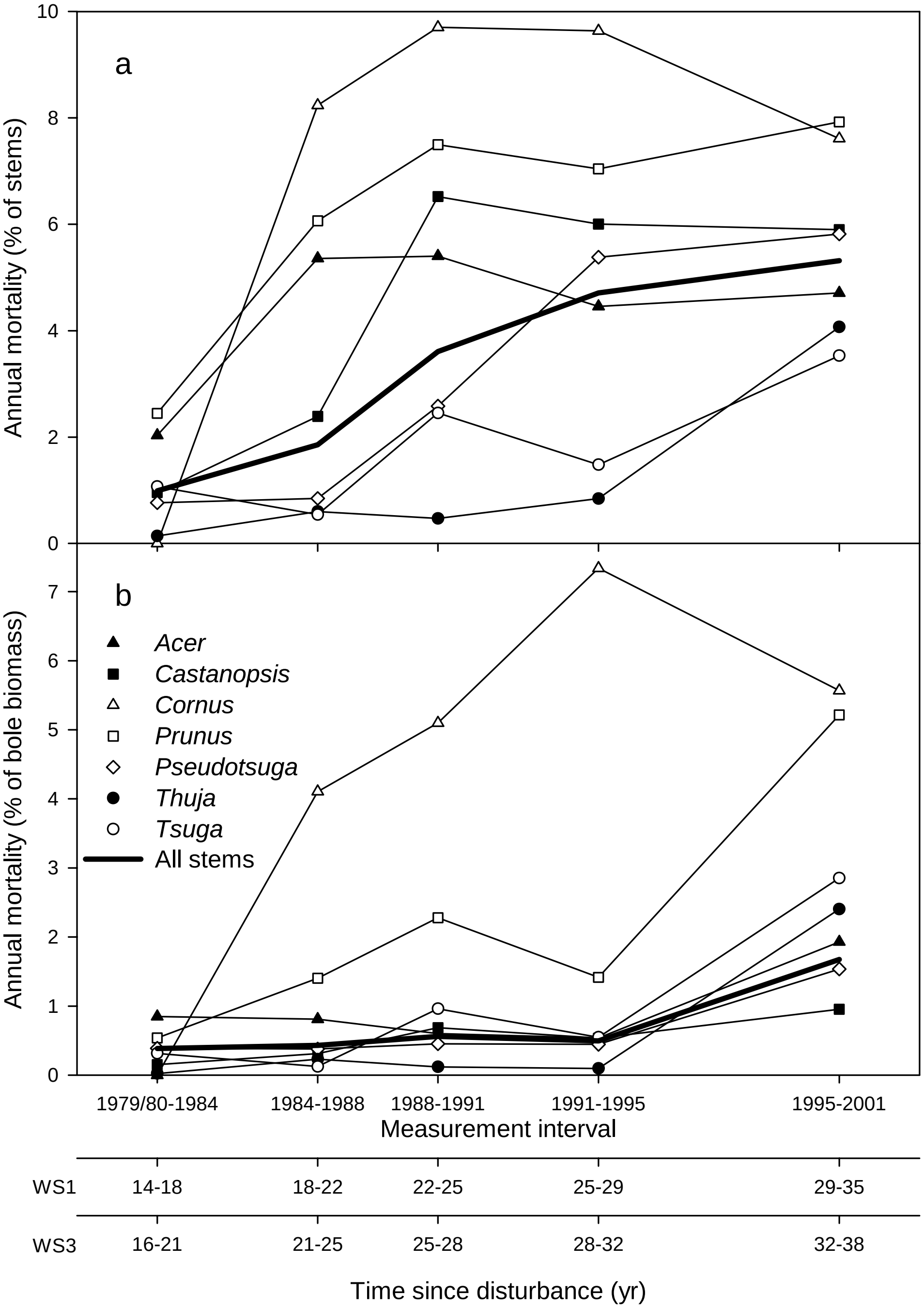

FIG. 5. Annual mortality rates of the seven common tree species and all stems combined during each measurement interval. Rates are based on proportions of (a) stems and (b) bole biomass by species. Data from both watersheds combined with points representing 2-3 yr intervals of time since disturbance. Secondary axes represent time since disturbance for each watershed.

Causes of mortality

Watershed-scale patterns. – Of a total of 7,146 recorded mortalities (tagged trees only), 26% could not be assigned a cause (Table 1). Among the remainder, suppression was the most frequent form of mortality (51% of tagged stems) and mechanical damage accounted for 18% of stems (Table 1). None of the remaining causes of mortality contributed to more than 2% of stems. A very different ranking of importance emerged for mortality expressed as loss of bole biomass: mechanical damage accounted for 51% of total mortality and suppression only 14% (Table 1). This reversal reflects the strong contrast in diameter distributions of populations lost to suppression and mechanical damage (Fig. 6). Suppression killed many small-diameter stems (quadratic mean diameter [QMD] of 3.4 cm); mechanical damage killed fewer, but considerably larger stems (QMD of 8.4 cm). Although a cause could not be assigned to one-quarter of all mortality, diameter distributions of "unknown" and "known" populations did not differ (Kolmogorov-Smirnoff test, *P*=0.50). Thus, omission of unknown cases from these comparisons is not likely to bias our estimates of the differences in vulnerability of stems to suppression or mechanical damage. Pathogen-induced mortality accounted for 4% of total dead biomass and typically removed the largest trees (QMD of 11.3 cm).

TABLE 1. Annual mortality by cause during each sampling interval (or time since disturbance) expressed as stem density (top) and bole biomass (bottom).

Interval	1979-84	1984-88	1988-91	1991-95	1995-01	Total
Time (yr)	14-21	18-25	22-28	25-32	29-38	14-38
Density (stems ha^{-1} yr^{-1})						
Suppression	0.8	3.8	44.3	88.5	56.9	41.7
Mechanical	2.2	0.9	21.8	7.6	33.0	15.1
Slope failure	0.2	0.4	1.8	0.3	5.0	1.9
Pathogen	t[2]	0.2	0.7	0.6	1.4	0.7
Animal	0.1	0.1	0.7	0.4	0.3	0.3
Old growth[1]	4.8	2.5	0.2	0.4	0.0	1.6
Unknown	9.7	25.5	13.4	25.1	24.2	21.1
Total	17.8	33.2	82.9	122.9	120.8	82.4
Bole biomass (Mg ha^{-1} yr^{-1})						
Suppression	t	0.002	0.030	0.104	0.168	0.075
Mechanical	0.003	0.002	0.125	0.043	0.840	0.276
Slope failure	t	0.001	0.005	0.003	0.050	0.016
Pathogen	t	0.014	0.015	0.019	0.042	0.021
Animal	t	t	0.001	0.014	0.008	0.005
Old growth	0.010	0.008	0.001	0.001	0.000	0.004
Unknown	0.011	0.053	0.039	0.105	0.334	0.138
Total	0.025	0.079	0.216	0.290	1.443	0.536

[1] Crushed beneath old-growth trees (see *Methods: Tree measurements*)

[2] t = trace, <0.1 stems ha^{-1} yr or <0.001 Mg ha^{-1} yr^{-1}

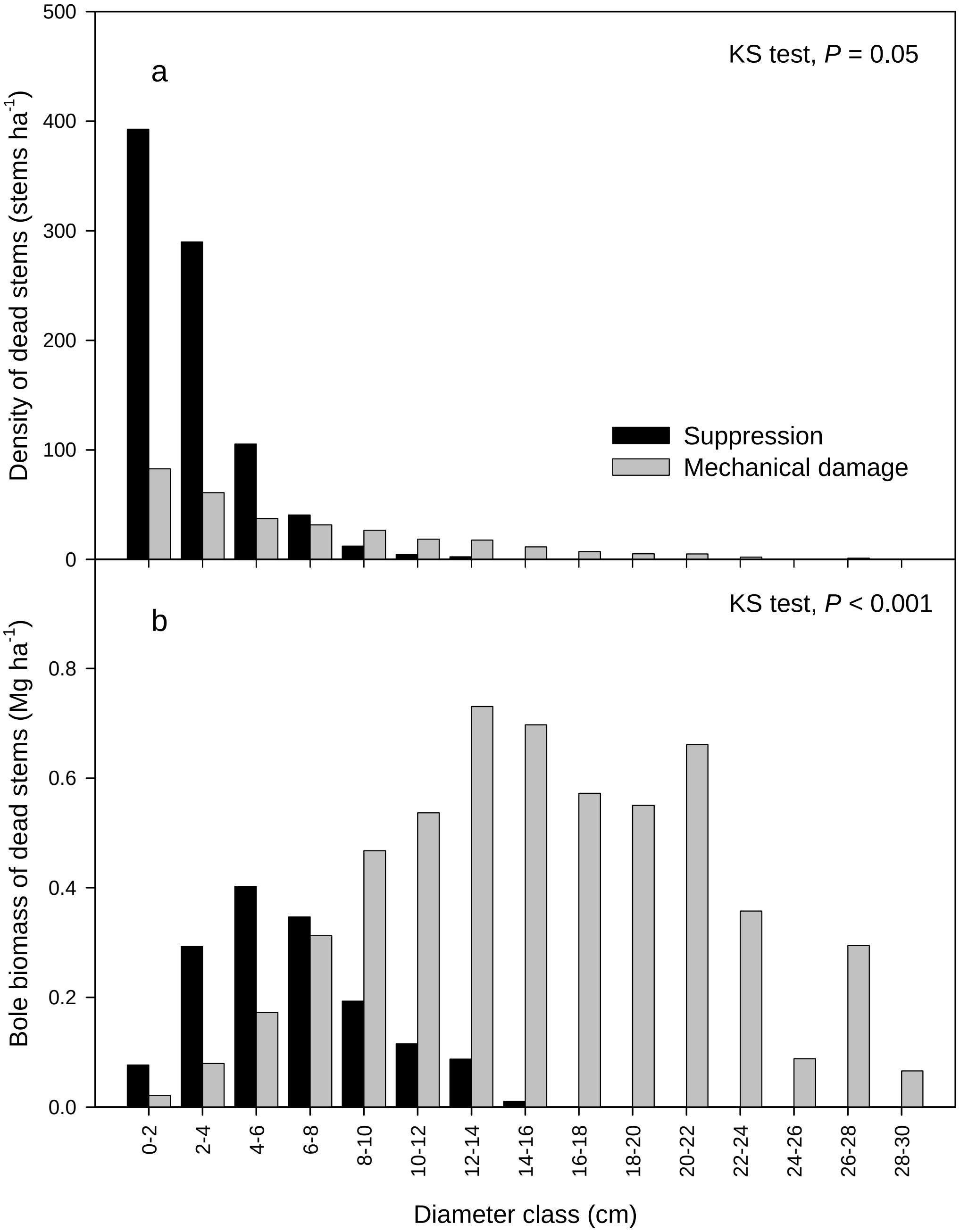

FIG. 6. Distribution of cumulative mortality among diameter classes attributable to suppression and mechanical damage. Mortality is expressed as (a) density of stems and (b) bole biomass. Data for both watersheds are combined. P values are from Kolmogorov-Smirnov (KS) tests on the distributions of mortality expressed as density of stems and bole biomass.

Spatial distributions and temporal trends. – The primary causes of mortality showed considerable variation in space and time. Suppression mortality was broadly distributed across both watersheds (82% of plots). Rates of stem loss peaked between 25-32 yr, but loss of biomass increased continually as trees increased in size (Table 1). In contrast, mortality attributable to physical causes was spatially patchy and episodic. Mechanical damage occurred in 56% of plots, with 86% of stems and 98% of biomass lost during two of the five sampling intervals (Table 1). These losses reflect the effects of major winter storms preceding the 1991 and 2001 measurements. Mortality attributable to slope failure was also episodic and localized, occurring in 5% plots. In addition, two old-growth trees fell into harvest units from adjacent forest during the first two sampling intervals. Although only four plots were affected, these events accounted for 8-27% of dead stems and 10-40% of dead biomass during these periods (Table 1). In both instances, a number of damaged trees succumbed to mortality during subsequent measurement intervals.

Occurrence of pathogen-induced mortality was limited in time and space. Loss of *Cornus* to dogwood anthracnose (*Discula destructive*) was not recorded until the second decade of observation and in only 7% of plots that contained *Cornus*. Loss of *Pseudotsuga* to root rot (primarily *Armillaria ostoyae*) was not significant until the final sampling interval (29-35 yr) and was restricted to 5% of plots (primarily at the top of WS1). Thirteen plots (7%) had no mortality during the study period.

The proportion of plots that experienced major (>20%) declines in stem density between measurements increased with time, with losses due to a combination of suppression and mechanical damage (left panel, Fig. 7). Declines in biomass were less frequent: most plots exhibited increases of 20-60%. However, the proportion of plots that experienced declines increased with time; these losses were attributable solely to mechanical damage (right panel, Fig. 7).

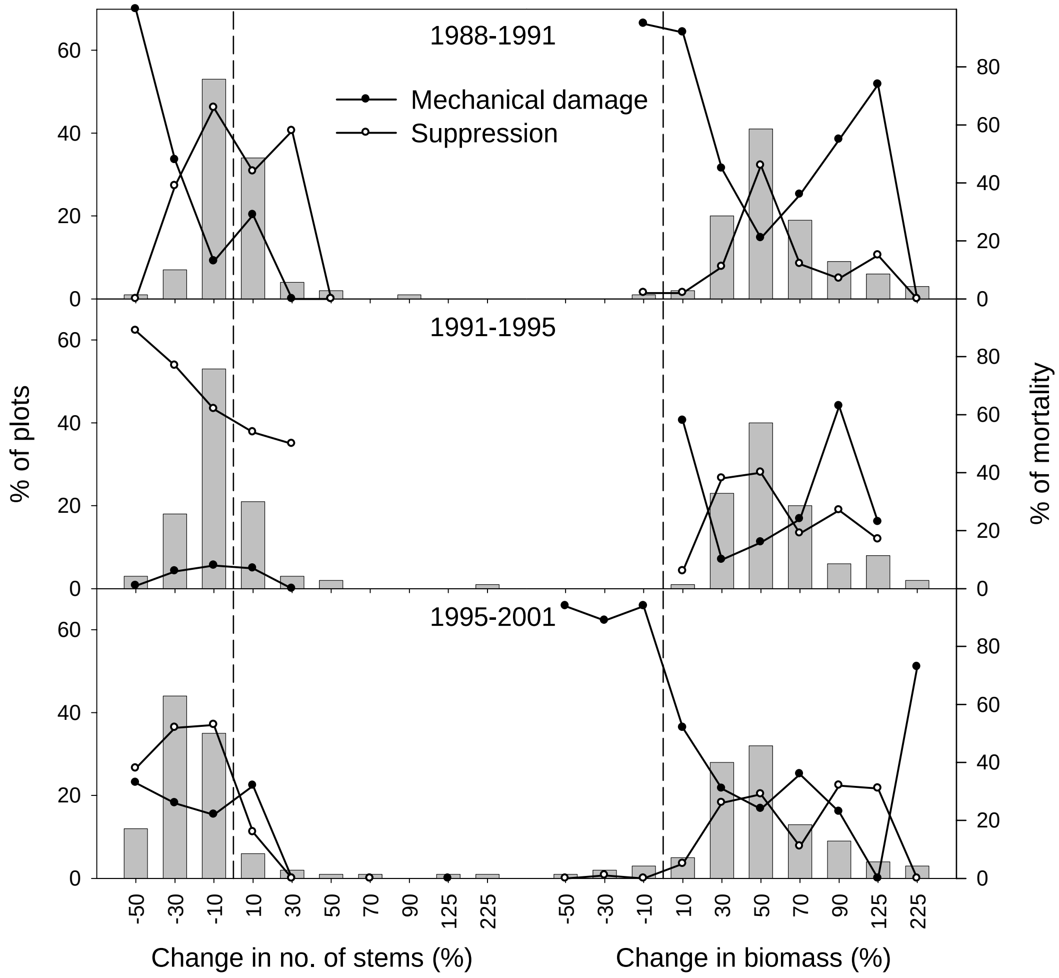

FIG. 7. Percentage of plots (left axis) showing declines and increases in stem density (histograms, left) and bole biomass (histograms, right) during each of the last three measurement intervals. Solid lines indicate the relative contribution of suppression (open circles) and mechanical damage (closed circles) to mortality (right axis) within each set of plots. Dashed vertical lines separate negative and positive changes in density or biomass. Abscissa values represent mid-points of 20% classes (except for 125 [100-150%] and 225 [150-300%]). Data from both watersheds are combined.

Species differences. – Causes of mortality varied significantly among species. Three general patterns were observed corresponding to hardwoods, *Pseudotsuga*, and shade-tolerant conifers. For hardwoods, suppression was by far the dominant form of mortality, both in numbers and bole biomass (Table 2). Rates of suppression were undoubtedly higher than reported. Clump stems, which are not included in these estimates, were commonly lost through "self-pruning." In addition, much of the hardwood mortality recorded as "unknown" was likely due to suppression because there was no evidence of physical damage or disease.

For *Pseudotsuga*, suppression was three times more frequent than mechanical damage, but mechanical damage yielded more than four times the loss of bole biomass (Table 2). Mortality of the shade-tolerant conifers, *Tsuga* and *Thuja*, was dominated by mechanical damage, both in numbers and biomass (Table 2).

Environmental and biotic correlates of mortality

The regression tree analyses of cumulative mortality produced very different models for suppression and mechanical damage. In the suppression model (86% reduction in deviance; Fig. 8a), mortality was partitioned by initial density at several levels (greater at higher density), aspect (greater on north and east aspects), insolation (greater mortality in shadier plots), and pre-disturbance vegetation (limited proportion of deviance explained). In the mechanical-damage model (58% reduction in deviance; Fig. 8b), the first partition was also on stem density, but it accounted for considerably less of the total deviance explained. Additional significant predictors included aspect (greatest on north and east aspects), watershed (greater in WS3 than WS1), and soil type (lower on stony soils and talus, but with little explanatory power). Slope, distance to forest edge, distance to southern ridgeline, and biomass at initial measurement were not significant predictors.

TABLE 2. Percentage of mortality attributed to suppression (Supp), mechanical damage (Mech), and "unknown" (Unkn) for the seven common tree species. Values are the total number (*n*) of tagged stems that died over the study period and the percentages in numbers of stems and bole biomass.

		Stems (%)			Bole biomass (%)		
Species	*n*	Supp	Mech	Unkn	Supp	Mech	Unkn
Prunus emarginata	710	42.9	6.5	49.3	51.1	12.5	33.9
Castanopsis chrysophylla	578	48.5	2.6	48.4	49.5	13.2	35.6
Cornus nuttallii[1]	117	35.6	9.7	47.8	25.3	9.0	48.8
Acer macrophyllum	316	26.3	13.6	58.4	11.0	10.5	78.1
Pseudotsuga menziesii[2]	4399	59.3	18.8	18.5	12.5	58.0	22.6
Thuja plicata	144	21.1	67.7	11.3	2.6	94.5	2.9
Tsuga heterophylla	804	29.1	51.5	13.2	6.1	75.6	15.8

[1] For *Cornus*, a pathogen (dogwood anthracnose) was responsible for mortality of 6.0% of stems and 16.3% of biomass.

[2] For *Pseudotsuga*, pathogens (root rot) were responsible for mortality of 1.0% of stems and 4.8% of biomass.

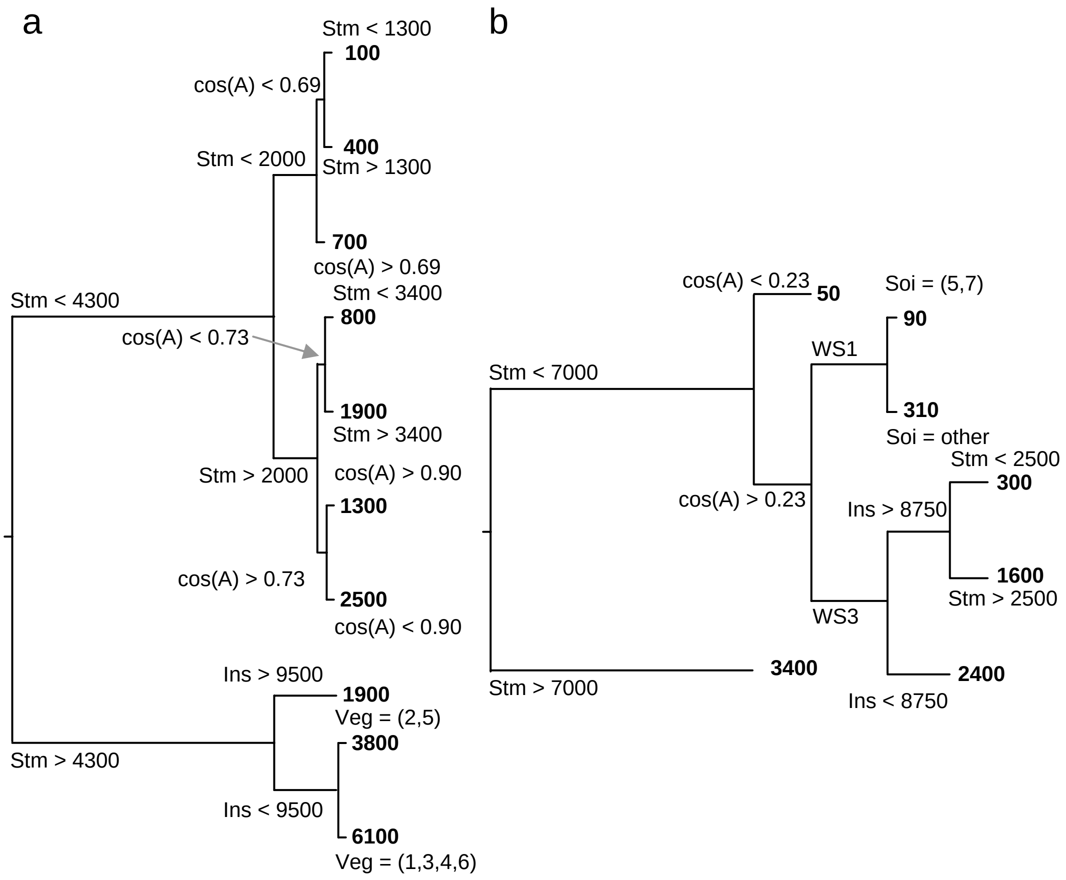

FIG. 8. Regression-tree results illustrating the distribution of mortality in both watersheds. Separate models are shown for (a) suppression (percentage deviation explained = 0.86) and (b) mechanical damage (percentage deviation explained = 0.58) based on environmental predictors and biotic predictors (density of live stems and bole biomass at the first measurement). Values in bold at the ends of the trees are cumulative mortalities (stems ha^{-1}). Threshold values for predictors are shown along the branches. Predictors are coded as: cos(A), cosine transformation of aspect (see *Methods: Data reduction and analysis*); Ins, insolation (MJ m^{-2} day^{-1}); Soi, soil type (1 = Frissell/McKenzie River, 2 = Limberlost, 3 = Andesite colluvium, 4 = Budworm/Slipout, 5 = Stony Frissell/Stony Limberlost, 6 = Talus; Rothacher et al. 1967); Stm, stem density (stems ha^{-1}); Veg, plant community (1 = *Corylus cornuta – Gaultheria shallon*, 2 = *Rhododendron macrophyllum – Gaultheria shallon*, 3 = *Acer circinatum – Gaultheria shallon*, 4 = *Acer circinatum – Berberis nervosa*, 5 = *Coptis laciniata*, 6 = *Polystichum munitum*);. WS1/WS3, watershed. The length of horizontal line segments in each tree is proportional to the proportion of deviation explained.

DISCUSSION

Long-term measurements in these experimental watersheds provide abundant evidence that current models of forest succession paint an overly simplistic picture of the early development of *Pseudotsuga* forests. More than 20 yr of density, growth, and mortality data reveal spatial and temporal variation that are not possible to discern from space-for-time substitutions. Sample plots followed multiple trajectories of structural development, reflecting differences in initial composition, variation in recruitment, and diversity in the timing and causes of mortality. The spatial and temporal breadth of these data allow us to re-examine many of the assumptions and uncertainties implicit in current successional models. At the same time, it is important to recognize that this represents a single study of two watersheds. Despite the size and diversity of habitats represented by these sites, care must be taken in generalizing to other forest types or locations.

Re-examining compositional and structural patterns in young forests

It is generally assumed that if present in the species pool, early successional hardwoods dominate forest establishment, either through vegetative sprouting (Harrington 1990, McDonald and Tappeiner 1990, McKee 1990, McLomore 1990, Minore and Zasada 1990) or recruitment and rapid growth of seedlings (Marks 1974, Harrington 1990). Both strategies were evident in this study: abundant basal sprouting of *Acer*, *Castanopsis*, and *Cornus*, and locally dense establishment of *Prunus* from a persistent soil seedbank (Oakley and Franklin 1998). However, dominance by hardwoods was largely restricted to south-facing slopes and areas with shallower soils. *Alnus rubra,* which has the potential for abundant recruitment and early dominance in more coastal forests in this region (Newton and Cole 1994, Hibbs and Bonner 2001, Binkley 2003), was largely restricted to riparian habitats in these sites.

Given the inherent tradeoff between rapid juvenile growth and longevity (Grime 1979), I expected to see gradual loss of hardwood species with closure of the canopy by *Pseudotsuga*. However, long-term trends revealed a somewhat surprising result. Although densities declined after an early peak (18-25 yr), biomass increased consistently for nearly all species of hardwoods. Deciduous (*Acer*) and evergreen (*Castanopsis* and *Arbutus*) species showed similar growth patterns: vigorous basal sprouting, differential growth of neighboring shoots, and gradual "self-pruning" of smaller, subordinate stems. Surviving stems of *Acer* were particularly large, forming tall and very broad canopies, often to the exclusion of other species. Not only did biomass show continuous increases, but for *Acer* and *Castanopsis*, mortality rates during the last measurement interval were less than, or comparable to, rates for *Pseudotsuga*. Clearly, presence in the pre-disturbance community, ability to accumulate biomass during canopy closure, declining mortality rates, and longevities spanning centuries (Keeler-Wolf 1988, McKee 1990) suggest the potential for long-term persistence of hardwoods in these forests well past canopy closure.

The early establishment and abundance of shade-tolerant conifers in these forests also contrasts with traditional stand development models. Their reestablishment is typically assumed to take decades, if not centuries after disturbance (Oliver and Larson 1996, Acker et al. 1998a, Franklin et al. 2002), with recruitment limited by environmental or edaphic constraints, size or intensity of disturbance, or dispersal limitation (Harmon and Franklin 1989, Busing et al. 1995, Schrader 1998, Beach and Halpern 2001, Keeton and Franklin 2005). In fewer than four decades, *Tsuga* comprised >20% of all stems and as a group, shade-tolerant conifers dominated nearly 20% of the plots by density. In some plots, *Tsuga* was dominant at every measurement. Rapid establishment of *Tsuga* was facilitated by the proximity and abundance of old-growth seed sources along harvest-unit boundaries, particularly on cooler, moister, north-facing slopes. Occasional advanced regeneration was also observed, primarily in microsites that escaped broadcast burning (Halpern 1989). These disturbance refugia were very important for *Taxus,* whose dispersal potential is poor; once extirpated, reestablishment in the forest understory can take centuries (Busing et al. 1995).

Plot-level comparisons of simple structural attributes (stem density and biomass) highlight extreme spatial variation in the pace and "intensity" of canopy closure in these forests. This runs counter to the common perception – possibly shaped by the "plantation" model of stand development – that canopy closure occurs uniformly and rapidly in *Pseudotsuga* forests. In these watersheds some plots regenerated quickly and densely to well over 5,000 stems ha^{-1}; others showed little if any regeneration even after 35 yr (Fig. 3). Accumulation of bole biomass showed similar variation among plots. This spatial heterogeneity of forest structure suggests that "horizontal diversification" in older forests — typically associated with gap-forming processes late in stand development (Franklin et al. 2002) — may begin earlier through processes unrelated to mortality.

Mortality patterns and processes

Estimates of total annual stem mortality in these forests were generally high, exceeding 5% during the fourth decade of stand development. These represent mean rates derived from measurement intervals of 3-6 yr, but annual variability may have been higher, particularly following years with storm events (see below). Early rates of mortality also differed markedly among species with different life histories: higher among hardwoods than shade-tolerant conifers, and intermediate for *Pseudotsuga* (Fig. 4). Interestingly, however, there was noticeable convergence in mortality rates over time. This reflects two phenomena: stabilizing or declining rates among hardwood clumps that experienced more intensive "self-thinning" earlier in succession and a noticeable increase in mortality of shade-tolerant conifers, not through suppression, but through crushing disturbance (see below). Mortality of *Pseudotsuga* increased to >5% during the fourth decade; this may represent peak mortality in these forests. In 45- to 80-yr old stands of similar composition, annual mortality of *Pseudotsuga* averaged 1.1-2.9% (Bible 2001). In mature and old-growth *Pseudotsuga/Tsuga* stands, rates appear to stabilize at ~0.5 – 0.9% (DeBell and Franklin 1987, Bible 2001). Comparable rates have been reported in mature and old *Picea/Tsuga* forests of the coastal Northwest (1.0 – 1.8%; Harcombe 1986, Pincheira 2004) and in deciduous forests of the eastern U.S. (0.5-1.4%; Runkle 2000, Busing 2005).

The results of this study support the conventional view that suppression is the most common form of mortality during early stand development. Suppression was observed in >80% of plots and was more than 2.5 times as frequent as mechanical damage (windthrow, stem snap, and crushing). However, biomass lost to mechanical damage was nearly four times that lost to suppression. The differing ecological consequences of suppression and mechanical damage underscore the need to distinguish between the two. Suppression typically killed smaller-sized hardwoods and *Pseudotsuga* through a gradual process of decline that released few resources, and likely led to greater uniformity of spacing (Kenkel 1988, He and Duncan 2000, Harris 2004, North et al. 2004). In contrast, mechanical damage was episodic and highly aggregated. Trees were windthrown, snapped or crushed, creating gaps of varying size with some plots losing as much as 30-50% of biomass during the last sampling interval. These large mechanical losses explain the abrupt changes in net primary productivity observed at final sampling (Fig. 1). Due to their canopy architecture and needle retention, conifers are more susceptible to snow loading and high winds (Boerner et al. 1988, Foster 1988b), and thus suffered greater damage than did hardwoods. *Tsuga* and *Thuja*, which were smaller and occupied subcanopy positions, were lost primarily through crushing disturbance.

A recent (2003) winter storm that post-dates the last measurement appears to have enlarged these gaps along unstable edges, illustrating the potential for continued gap expansion as these forests mature (Sprugel 1976, Wilson and Oliver 2000, Harcombe et al. 2004). Some gaps are large enough to facilitate recruitment of most tree species (including *Pseudotsuga*); however, it is conceivable that some will be filled by competitive understory species, thus inhibiting further regeneration (Veblen 1989, Rebertus et al. 1997). Anecdotal observations suggest that where they are not uprooted, crushed stems of *Tsuga, Thuja*, and *Taxus* are capable of reorienting branches to take advantage of increases in light, an adaptation to physical damage experienced in the understory of old-growth forests. Thus gap formation has the potential to locally reset or advance succession (Stewart 1986, Foster 1988b, Canham 1989, Spies et al. 1990, Holah et al. 1997, Sinton et al. 2000, Wright et al. 2003).

The effects of wind and ice storms that occur once or twice a decade have been studied extensively in other North American forest types (e.g., Stroempl 1971, Foster 1988b, Greenberg and McNab 1998, Van Dyke 1999, Platt et al. 2000, Ryall and Smith 2005). However, gap formation via wind or snowloading has not been considered an important ecological process in young *Pseudotsuga* forests (but see Acker et al. 2003). Damage is more likely to occur in taller (older) forests, which experience greater wind speed at greater height, and in denser stands in which increasing height-to-diameter ratios lead to greater instability of trees (Wilson and Archer 1979, Cremer et al. 1982, Smith et al. 1987, Foster 1988b, Mitchell et al. 2001). Snow loading of canopies and high-velocity wind storms occur frequently enough in the Pacific Northwest (Marks et al. 1998, Read 2005) to have the potential to induce significant mechanical damage in these forests. However, rain-on-snow events (Harr 1986) typically occur at higher elevations where snowpacks are more likely to accumulate. Convergence of multiple stressors in time and space clearly increases the likelihood of mechanical damage in these forests. During the 1996 storm event, deep snow had accumulated at low elevations, loading the canopies of *Pseudotsuga*. This was followed by strong wind and intense, persistent rain that saturated soils and destabilized root systems.

Regression-tree models supported my expectations that density-dependent mortality (Yoda et al. 1963) would be highly correlated with density prior to canopy closure. In contrast, environmental and edaphic attributes had little predictive value, although they may indirectly influence mortality through effects on tree recruitment and survival. For mechanical damage, I expected stronger physical controls associated with aspect (related to directionality of prevailing winds and distances to ridgelines), soil type (affecting root system depth and stability), and harvest unit size (as it influences wind speed and turbulence) (Fraser 1962, Savill 1998, Cremeans and Kalisz 1988, Ruel et al. 1998, Huggard et al. 1999, Sinton et al. 2000). Although mechanical damage was spatially aggregated, and relationships to aspect and size of harvest units were consistent with expectations, these environmental predictors contributed minimally to variation in mortality. Instead, as with the suppression model, initial stem density was the strongest predictor of mechanical damage. Although this outcome may simply reflect the fact that more stems can die where more stems are present, a biotic mechanism is equally plausible: tree stability is often reduced at higher densities (Cremer et al. 1982, Mitchell et al. 2001). Ultimately, mechanical damage is likely to be a complex response to physical and biotic conditions. It may be difficult to tease apart these influences in steep and heavily dissected landscapes where wind behavior and soil stability can vary at fine spatial scales.

For the conifer species, root-rot pathogens contributed minimally to tree mortality. Where present, however, root rot invariably killed larger *Pseudotsuga* and typically in small groups. Although consistent with the typical patterns of infection and spread in *Pseudotsuga* forests, mortality can be considerably greater (Childs 1970, Hansen and Goheen 2000, Filip and Ganio 2004). Pathogens played a more prominent role in the dynamics of *Cornus*, the only species to show a decline in biomass over the course of study. Infection by dogwood anthracnose, an introduced fungus, was responsible for >16% of biomass lost. However, it is likely that much of the *Cornus* mortality recorded as “unknown” was caused by anthracnose as early losses were likely to have gone undiagnosed. Anthracnose has been documented as a primary agent of mortality in dogwood throughout the midwestern and eastern U.S. (Williams and Moriarity 1999, Carr and Banas 2000, McEwan et al. 2000, Jenkins and White 2002). Although it has been observed on *Cornus nuttallii* in western forests (Salogga 1982), its distribution and ecological influence have not been described; this is the first study to quantify the demographic effects of infection in young forests of this region.

Relevance of post-harvest dynamics to natural successional processes

To what extent are developmental patterns in these clearcut, burned, and planted watersheds relevant to understanding natural successional processes in *Pseudotsuga* forests? Clearly, catastrophic fire would have left considerably more structure (primarily in the form of snags) and greater heterogeneity of post-disturbance environments, including patches of intact forest. Large areas of residual forest adjacent to WS1 and within WS3 may have functioned in similar ways, providing shade and an abundance of seed (Acker et al. 1998b, Traut and Muir 2000, Keeton and Franklin 2005). Natural seeding combined with widespread failure of artificial seeding and planting (particularly on WS1) resulted in a regeneration process shaped, in large part, by natural establishment. Although we cannot determine the origins of individual trees, early reports of germination and stocking surveys confirm that most *Pseudotsuga* originated from natural seeding. Shortly after planting, densities of surviving seedlings were estimated at 270 ha^{-1} (WS1) and 415 ha^{-1} (WS3), compared to average densities of *Pseudotsuga* of 1,948 and 1,680 ha^{-1} in 1988.

As agents of early forest mortality, fragmentation or toppling of snags and fire-scarred trees have the potential to enhance structural diversity and locally reset succession. The mortality incurred when old-growth trees fell from the forest edge offers insight into the potential importance of this process. Trees that were crushed accounted for a large percentage of the stems and biomass lost during these early sampling intervals. Historically, where catastrophic fire left a legacy of snags and damaged trees, falling boles could have been a significant source of mortality, one that played out over decades. In the current managed landscape where snags are typically felled during timber harvest or salvaged after wildfire (McClomb et al. 1993, Franklin et al. 2002), they play a relatively limited role.

Metrics of mortality and their ecological implications

Tree mortality is typically viewed from a demographic perspective, and hence mortality rates are usually expressed by changes in population density. However, the distinction between demographic and ecological expressions of mortality is critical in these forests. Suppression was the primary cause of mortality among hardwoods, whether expressed in numbers or biomass. Mechanical damage dominated both measures of mortality in shade-tolerant conifers. For both groups, neither the cause of death, nor its ecological consequence, was contingent on the metric of mortality. This was not the case for *Pseudotsuga*. Suppression dominated as a demographic process, and mechanical damage in ecological terms, removing significantly more biomass and creating greater spatial heterogeneity in structure. This contrast underscores the importance of long-term studies in forcing us to revisit what are often assumed to be tenets of basic ecological assumptions – in this case, that suppression is the "dominant" form of mortality in young, closed-canopy forests. Furthermore, it serves to blur the distinctions among developmental "stages" in these forests, emphasizing instead the continuity of pattern and process (Franklin et al. 2002). Gap-forming processes that contribute to structural complexity in old-growth (Spies and Franklin 1991, Franklin et al. 2002, Franklin and Van Pelt 2004, Wolf et al. 2004) can also be active in young forests.

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APPENDIX I: SPECIES DETAILS AND DEMOGRAPHY

Lists of tree and tall shrub species

Fourteen tree species and 24 tall shrub species were observed in sample plots in WS1 and WS3 during the study period (1979-2001) (Table 3). Tall shrub species are listed in Table 4. For details about their distributions and dynamics, see Halpern (1989).

TABLE 3. Tree species present in sample plots between 1979 and 2001. Nomenclature follows Hitchcock and Cronquist (1973).

Tree species	Species code	Common name
Conifers		
Abies amabilis	ABAM	Pacific silver fir
Pseudotsuga menziesii	PSME	Douglas-fir
Calocedrus decurrens	CADE3	Incense-cedar
Taxus brevifolia	TABR	Pacific yew
Thuja plicata	THPL	Western redcedar
Tsuga heterophylla	TSHE	Western hemlock
Hardwoods		
Acer macrophyllum	ACMA	bigleaf maple
Alnus rubra	ALRU	red alder
Arbutus menziesii	ARME	Pacific madrone
Castanopsis chrysophylla	CACH	giant chinquapin
Cornus nuttallii	CONU	Pacific dogwood
Populus trichocarpa	POTR2	black cottonwood
Prunus emarginata	PREM	bitter cherry
Rhamnus purshiana	RHPU	Cascara/bearberry

TABLE 4. Tall shrub species present in sample plots between 1979 and 2001.

Tall shrub species	Species code	Common name
Acer circinatum	ACCI	vine maple
Acer glabrum	ACGL	Rocky Mountain maple
Alnus sinuata	ALSI	Sitka alder
Amelanchier alnifolia	AMAL	serviceberry
Arctostaphylos columbiana	ARCO3	hairy manzanita
Ceanothus integerrimus	CEIN	deer brush
Ceanothus sanguineus	CESA	redstem ceanothus
Ceanothus velutinus	CEVE	snowbrush
Corylus cornuta var. *californica*	COCOC	California hazelnut
Garrya fremontii	GAFR	Fremont silktassel
Holodiscus discolor	HODI	ocean spray
Oemleria cerasiformus	OECE	indian-plum
Rhus diversiloba	RHDI	poison oak
Rhododendron macrophyllum	RHMA	Pacific rhododendron
Ribes lacustre	RILA	black gooseberry
Ribes sanguineum	RISA	red-flowering currant
Rosa gymnocarpa	ROGY	baldhip rose
Rubus leucodermis	RULE	black raspberry
Rubus parviflorus	RUPA	thimbleberry
Sambucus cerulea	SACE	blue elderberry
Salix scouleriana	SASC	Scouler's willow
Salix sitchensis	SASI2	Sitka willow
Vaccinium membranaceum	VAME	black huckleberry
Vaccinium parvifolium	VAPA	red huckleberry

Reclassification of plot attributes for regression-tree analyses

Plant community types. — Sample plots originally were assigned to one of six plant community types (Rothacher et al. 1967) or, because of limited understory development or unique composition, to an "unclassified" group. To maximize the number of plots used in analyses, nine unclassified plots were reassigned to one of the six defined types based on compositional similarity (Table 5).

TABLE 5. Classification of plots by plant community type. Nine "unclassified" plots were reassigned for regression-tree analyses.

Data code	Plant community type	Original no. of plots	No. of plots after reassignment
1	*Corylus cornuta – Gaultheria shallon* (COCO/GASH)	12	13
2	*Rhododendron macrophyllum – Gaultheria shallon* (RHMA/GASH)	31	31
3	*Acer circinatum – Gaultheria shallon* (ACCI/GASH)	18	19
4	*Acer circinatum – Berberis oregana* (ACCI/BENE)	45	48
5	*Coptis laciniata* (COLA)	35	35
6	*Polystichum munitum* (POMU)	43	47
7	Unclassified	9	– *

* The following plots (watershed, harvest unit, transect, plot) were reclassified: 1,1,2,02 as COCO/GASH. 1,1,4,18 as ACCI/GASH. 1,1,4,03; 3,1,2,02; and 3,3,2,07 as ACCI/BENE. 3,1,4,04; 3,2,2,04; 3,3,1,05; and 3,3,2,04 as POMU.

Soil types.— Sample plots were originally assigned to one of nine soil types (Rothacher et al 1967). To improve interpretability of regression-tree analyses, the number of soil types was reduced by combining types with similar properties (T. Dyrness, *personal communication*) (Table 6). The following types were combined: McKenzie River and Frissell, Slipout and Budworm, Stony Frissell and Stony Limberlost (the latter two derive from different parent material, but are similar in their shallow and poorly developed profiles).

TABLE 6. Classification of plots by soil type.

Original data code	Soil type	Original no. of plots	New data code	No. of plots after combining types
1	Frissell	42	1	43
2	Limberlost	42	2	42
3	Andesite colluvium	27	3	27
4	McKenzie River	1	–	–
5	Budworm	11	4	15
6	Slipout	4	–	–
7	Stony Frissell	25	5	48
8	Stony Limberlost	23	–	–
9	Talus	18	6	18

Aspect.— For 5 of the original understory quadrats (2 x 2 m) aspect was classified as "flat" (no aspect). To ensure presence of the associated tree plots in the regression-tree analyses, aspect was reevaluated for these plots. Using a digital elevation model, aspect was calculated from the shortest line between the two 10-m contour intervals bordering each plot. This resulted in the following values: plots 1,1,6,16; 1,1,6,18; 3,2,4,03; 3,2,4,04: west; plot 3,2,1,03: north.

DBH-DBA regressions

To compute total basal area and bole biomass, diameters of stems measured at the base (dba) were converted to diameters at breast height (dbh) using species-specific regression equations. The population of stems measured simultaneously for dba and dbh were used to develop these equations. The range of dba values that needed to be interpolated were examined for each species. All paired dba-dbh values to be used as predictors were selected if their dba values were within 10% of the required dba prediction interval. Separate dbh-dba models were considered for stems in WS1 and 3, but only for *Pseudotsuga menziesii* did the regression slopes differ significantly (partial F-test, $P < 0.001$)(conifers; Fig. 9, hardwoods; Fig. 10).

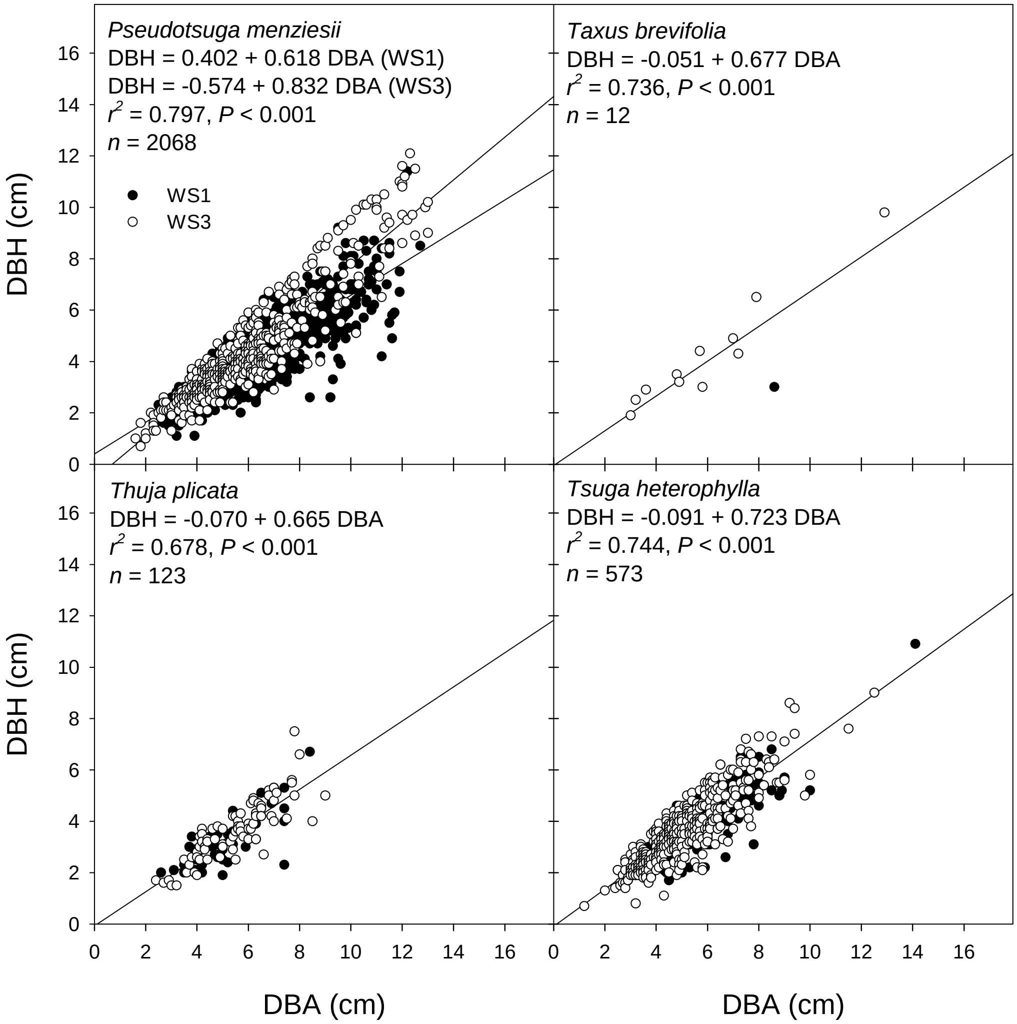


FIG. 9. Relationships between diameter at breast height (DBH) and diameter at the base (DBA) for coniferous species in WS1 and 3. The relationship for *Pseudotsuga menziesii* represents a single regression model – hence a single r^2. The block effect on slope and intercept (partial F-test, $P < 0.001$) has been converted into two separate DBA-DBH equations for clarity of presentation.

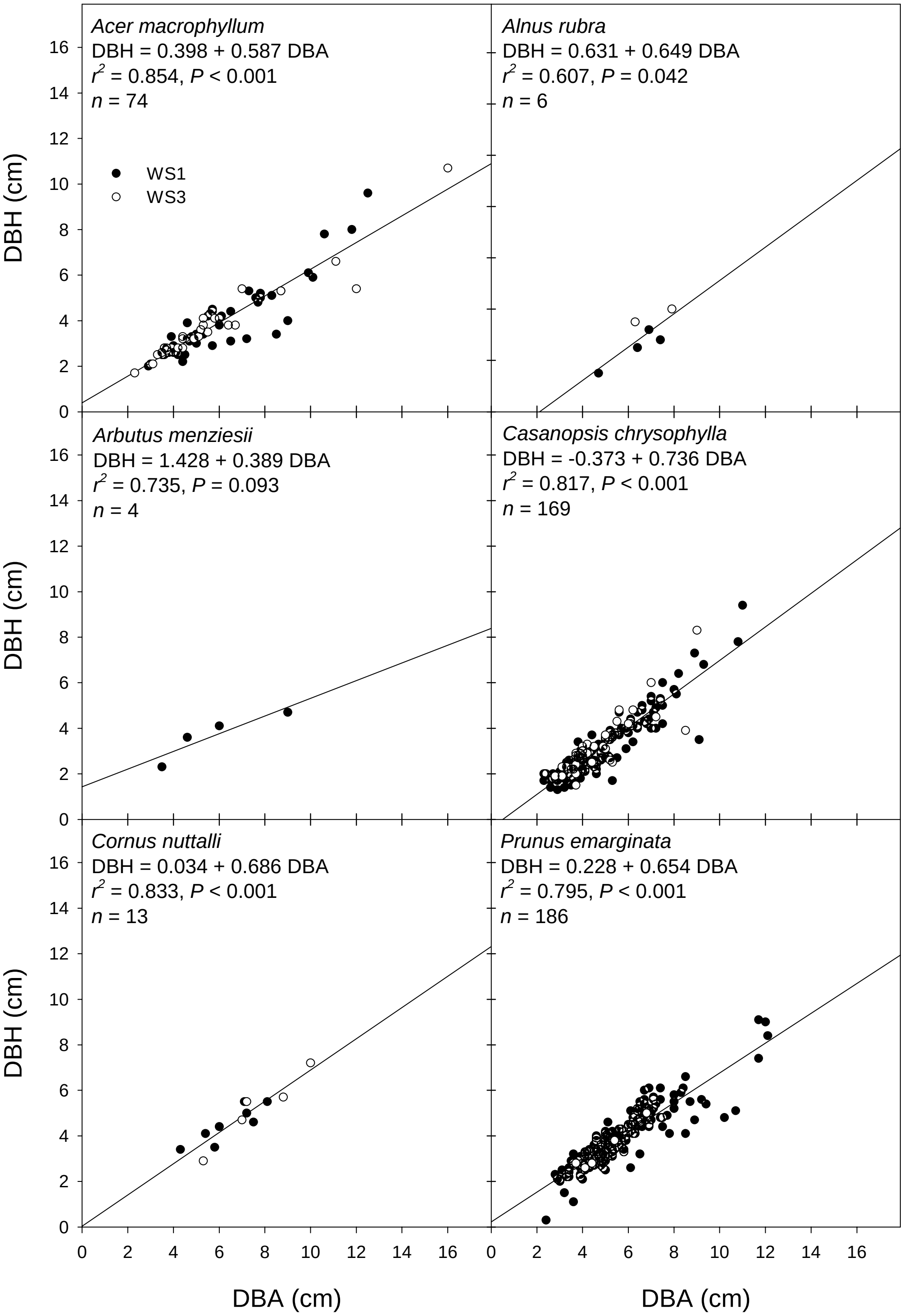


FIG. 10. Relationships between diameter at breast height (DBH) and diameter at the base (DBA) for hardwood species in WS1 and 3.

Changes in diameter-class structure through time

The diameter-class distributions of all stems at each sampling date are illustrated in Fig. 11. The distributions for WS1 and 3 are plotted separately.

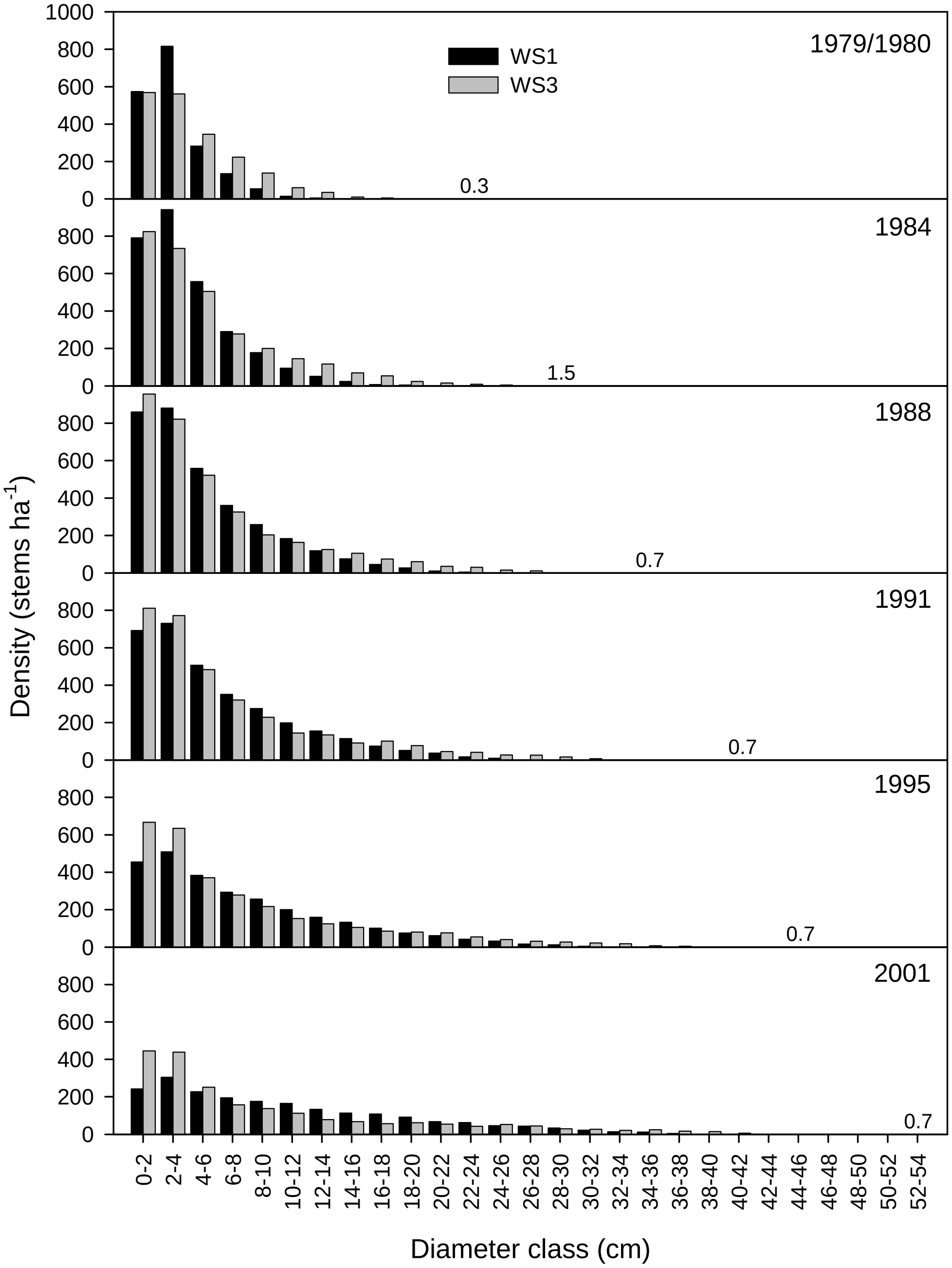


FIG. 11. Changes in diameter-class distributions of all stems in WS1 and 3 over time. The largest trees are represented by the numerical values above the axis.

Comparison of survivors and mortalities

The diameter-class distributions of all stems living in 2001 and cumulative mortalities are illustrated in Fig. 12. Watersheds 1 and 3 are plotted together.

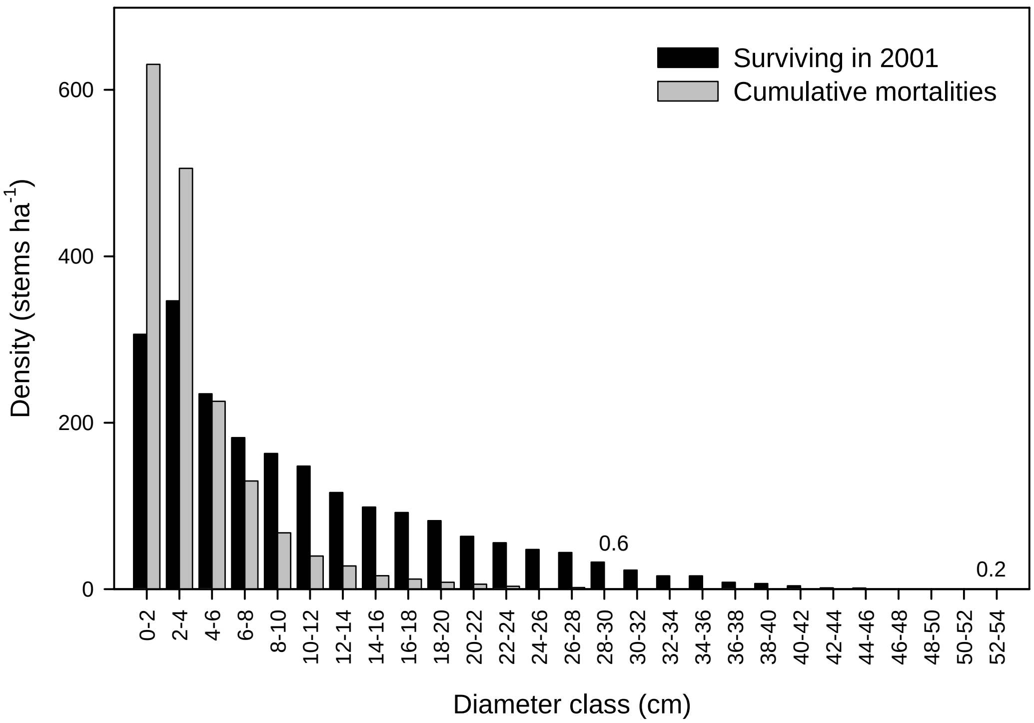


FIG. 12. Diameter-class distributions of trees surviving in 2001 and cumulative mortalities. The largest trees of each type are represented by the numerical values above the axis.

APPENDIX II: METHODS FOR CALCULATING BOLE BIOMASS

Calculations of bole biomass followed the methods of Acker et al. (2002). This first required an estimate of diameter at breast height (dbh) for all stems. For trees with only measurements of basal diameter (dba), dbh was estimated from species-specific regression equations developed from stems that had been measured at both points (Appendix I). For clump (tallied) stems, dbh was assigned the midpoint of the size class: 1.5 cm for stems 0.1 – 3.0 cm and 4.0 cm for stems 3.1 – 4.9 cm. Biomass calculations followed three general forms, depending on species.

1. Hardwood species (*Acer macrophyllum, Arbutus menziesii*, and *Castanopsis chrysophylla*).— For these species, I first estimated bole volume (m^3) using an equation of the form:

$$Volume = B_0 * DBH^{B_1} * Height^{B_2} \qquad [3]$$

Height (m) was computed from diameter using the equations of Garman et al. (1995):

$$Height = 1.37 + B_0 * \left(1 - e^{B_1 * DBH}\right)^{B_2} \qquad [4]$$

Species-specific parameters for these equations are listed in Tables 7 and 8.

TABLE 7. Parameters for estimating height from dbh for *Acer macrophyllum* (ACMA), *Arbutus menziesii* (ARME), *and Castanopsis chrysophylla* (CACH) (from Garman et al. 1995).

Species	Eco-region	B_0	B_1	B_2
ACMA	North Oregon Cascades	30.41311	-0.034245	0.682100
ARME	South Oregon Cascades	24.212490	-0.033914	0.891708
CACH	North Oregon Coastal	40.664790	-0.017775	0.873626

TABLE 8. Parameters for estimating volume from diameter and height for *Acer macrophyllum* (ACMA), *Arbutus menziesii* (ARME), *and Castanopsis chrysophylla* (CACH) (from the computer software, BIOPAK; Means 1994).

Species	BIOPAK equation no.	B_0	B_1	B_2
ACMA	654	0.0000718042	2.224620	0.575610
ARME	674	0.0000378129	1.992950	1.015320
CACH	663	0.0001169607	2.022320	0.686380

Finally, volume was converted to bole biomass by multiplying by wood density. Species-specific densities were provided by Mark Harmon (*personal communication*) from the literature: *Acer macrophyllum* (0.44 g cm^{-3}), *Arbutus menziesii* (0.56 g cm^{-3} for wood, bark mass assumed negligible), and *Castanopsis chrysophylla* (0.42 g cm^{-3}).

2. *Alnus rubra*.— Bole biomass (g) was computed directly using equation 266 from the software, BIOPAK (Means 1994), as follows:

$$Biomass = e^{3.97} + 2.56^{ln(DBH)} \qquad [5]$$

3. Pseudotsuga menziesii, Thuja plicata, and *Tsuga heterophylla.*— Four steps were necessary to estimate bole biomass for these conifer species: (i) compute wood volume from dbh; (ii) compute bark volume from wood volume using species-specific bark/wood ratios; (iii) convert wood and bark volume to mass using archived density values; and (iv) sum wood and bark mass.

Local volume-dbh models were derived from individual-tree volume equations (Browne 1962) based on dbh and height (Table 9). Paired measurements of dbh and height were taken from a variety of datasets in the H. J. Andrews Experimental Forest (S. Acker, *unpublished data*). Acker et al. (2002) regressed volume computed with Browne's equations on dbh alone, yielding a new set of volume-dbh equations. For *Pseudotsuga menziesii*, separate models were developed for young, mature, and old-growth trees; the model for young trees was used in the current study. For *Thuj*a and *Tsuga*, a single (all-age) model was used for each species.

The resulting volume equations were of the form:

$$Volume = B_0 * DBH^{B_1} \qquad [6]$$

Species-specific parameters are listed in Table 9.

TABLE 9. Parameters for estimating volume from dbh for *Pseudotsuga menziesii* (PSME), *Thuja plicata* (THPL), and *Tsuga heterophylla* (TSHE) (from Acker et al. 2002).

Species	n	B_0	B_1	r^2
PSME	611	0.0001123560	2.509359	0.9718
THPL	64	0.0003339420	2.197256	0.9478
TSHE	272	0.0003720880	2.259720	0.9536

To generate species-specific bark volume/wood volume ratios, Acker et al. (2002) computed mean ratios (Table 10) using data from an optical dendrometer dataset representing sites in the western Cascade Range. Values for wood and bark density were taken from the same dataset. Data are online at Oregon State University Forest Science Data Bank:

http://www.fsl.orst.edu/lter/data/abstract.cfm?dbcode=TV009&topnav=97).

TABLE 10. Bark-to-wood-volume ratios and bark and wood densities for *Pseudotsuga menziesii* (PSME), *Thuja plicata* (THPL), and *Tsuga heterophylla* (TSHE) (from Acker et al. 2002).

		Bark : wood ratio		Density (g cm^{-3})	
Species	*n*	Mean	S.D.	Bark	Wood
PSME	215	0.290	0.138	0.438	0.452
THPL	52	0.082	0.055	0.333	0.312
TSHE	208	0.124	0.054	0.415	0.421

4. Species substitutions.— For species lacking volume or biomass equations, substitutions were made based on knowledge of growth form and wood density. Equations were substituted as follows: (i) *Pseudotsuga menziesii* for *Abies amabilis*; (ii) *Tsuga heterophylla* for *Taxus brevifolia*; (iii) *Tsuga heterophylla* for *Calocedrus decurrens*; and (iv) *Alnus rubra* for *Cornus nuttallii, Prunus emarginata*, and *Rhamnus purshiana*. Substitutions were not made for wood or bark density except for *Taxus brevifolia. Taxus* was assigned a bark density of 0.415 (*Tsuga heterophylla*) and a wood density of 0.60 g cm^{-1} (M. Harmon, *personal communication*). Implementation software is included as Appendix VI.

APPENDIX III: PERMANENT PLOT LOCATIONS AND ATTRIBUTES

The locations of plot centers were determined by a combination of field measurement and interpolation. Plots were visited between 1 and 9 July 2004. GPS data were taken with a Trimble Asset Surveyor and a TDC-1 data logger. Each data point was measured in 3D mode with over 200 samples. Data were taken with a backpack-mounted unit standing within 1 m of the rebar marking the plot center, or an approximation of plot center if the rebar could not be located. GPS signals could not be received at some plot centers. Locations for these plots were interpolated. Most interpolated plot centers are within 60 m of a measured plot center. Plots in WS1, Transect 5 and WS3, Unit 2 were interpolated from a single point and transect azimuth. A total of 91 plots were located with GPS and 102 were interpolated. Data were post processed with Trimble Office software. Differential correction data in RINEX format were obtained from the closest reference station, OBEC Consulting Engineers (Eugene, Oregon). All data were referenced to NAD27, UTM.

Plot elevations were extracted from GIS data maintained at HJA. The base map is a 10-m DEM. Digital orthoquads from 2000 were used for images. ESRI software was used for the GIS manipulations. Plots and transects are shown superimposed over the orthoquad in Fig. 13.

Table 11 includes plot locations, elevations, slope, aspect, soil type and pre-disturbance plant community (Rothacher et al. 1967).

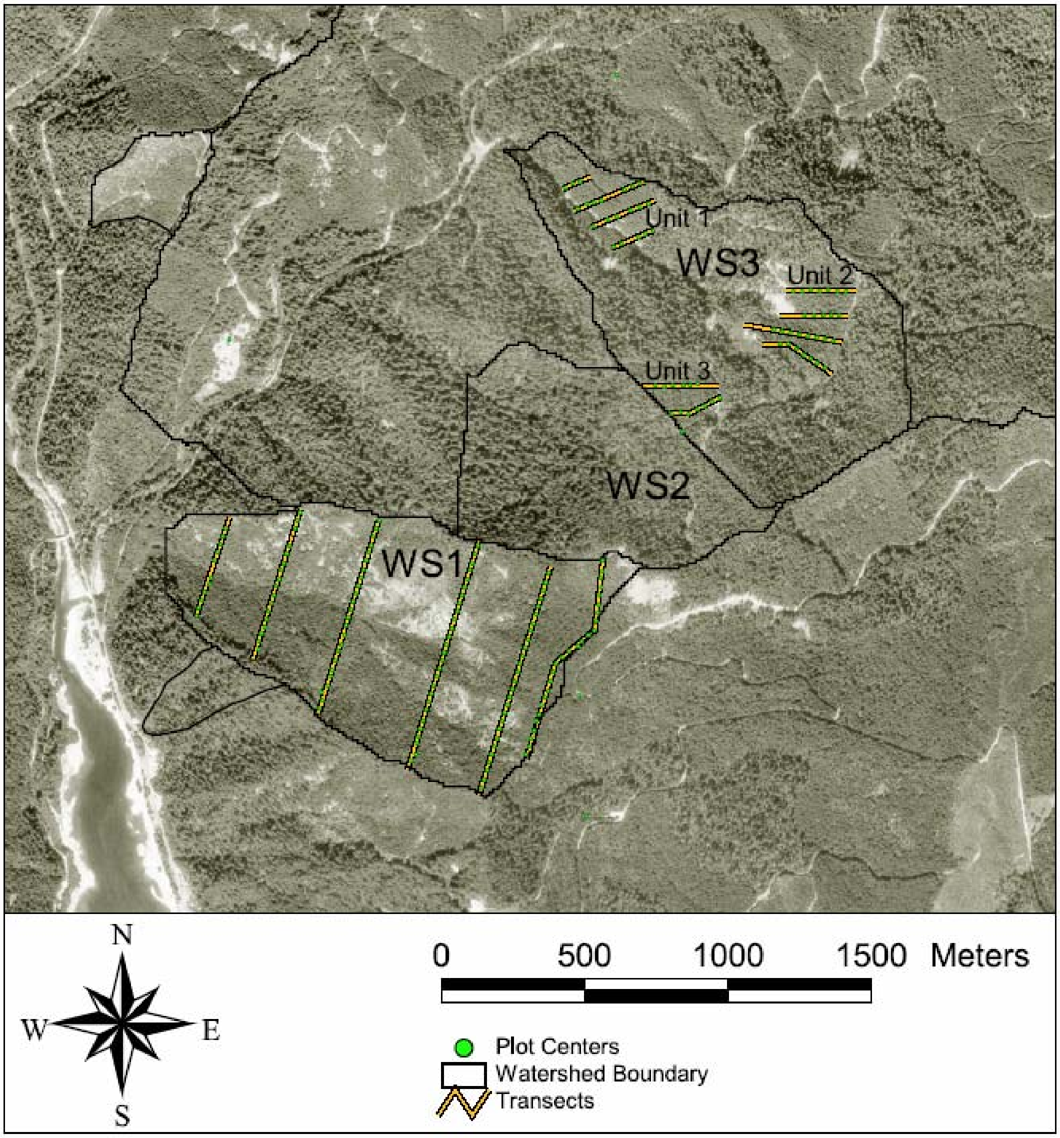


FIG. 13. HJA Experimental Forest, Watersheds 1, 2 and 3. WS3 was harvested in three units. Base map is generated from two digital orthoquads from overflights in the year 2000 (USGS reference B244122 and B344122). WS2 is an old-growth control. Transects and plot locations are shown. Dark outlines represent the hydrologic boundaries of the watersheds.

TABLE 11. Plot locations and characteristics. For frequency distributions of soil type and pre-disturbance plant community type, see Table 5 and Table 6.

Watershed, unit, transect, plot	Easting (UTM)	Northing (UTM)	GPS location[§]	Elevation (m)	Slope (°)	Aspect	Soil type[†]	Plant comm.[‡]
Watershed 1								
1,1,1,01	559594	4894983	M	550.1	17	S	7	2
1,1,1,02	559584	4894956	M	533.2	31	S	7	3
1,1,1,03	559575	4894925	M	518.8	27	S	1	2
1,1,1,04	559566	4894897	M	495.1	17	SW	1	2
1,1,1,05	559554	4894871	M	479.2	33	SW	1	6
1,1,1,07	559542	4894813	M	488.9	37	N	7	6
1,1,1,08	559536	4894790	M	512.9	31	N	7	6
1,1,1,09	559520	4894763	I	531.8	31	N	7	6
1,1,1,10	559510	4894735	I	559.1	35	N	7	6
1,1,1,11	559500	4894707	I	575.2	31	N	1	5
1,1,1,12	559491	4894681	I	592.0	14	NW	1	5
1,1,2,01	559854	4895042	I	684.9	35	S	9	4
1,1,2,02	559844	4895013	I	663.7	31	S	9	7
1,1,2,03	559836	4894983	M	642.6	22	S	7	4
1,1,2,05	559816	4894922	M	591.4	27	S	7	1
1,1,2,06	559806	4894894	I	571.0	22	S	7	1
1,1,2,07	559797	4894863	I	553.8	17	S	7	6
1,1,2,08	559786	4894837	M	539.3	19	SW	1	1
1,1,2,09	559780	4894807	M	523.7	31	SW	1	6
1,1,2,10	559769	4894782	M	515.3	27	N	7	6
1,1,2,11	559762	4894752	M	530.1	31	N	7	6
1,1,2,12	559753	4894724	M	550.4	37	N	7	6
1,1,2,13	559742	4894695	M	570.1	35	N	7	6
1,1,2,14	559737	4894669	M	587.0	31	N	7	5
1,1,2,15	559729	4894639	M	610.2	27	N	9	5
1,1,2,16	559718	4894615	M	626.3	39	N	7	4
1,1,2,17	559710	4894590	M	643.5	39	N	1	1
1,1,2,18	559707	4894562	M	654.8	11	SW	1	2
1,1,3,01	560128	4895013	I	729.0	27	S	1	3
1,1,3,02	560118	4894985	I	720.0	27	S	1	3
1,1,3,03	560109	4894954	I	705.3	27	W	1	4
1,1,3,04	560101	4894925	I	695.2	29	SW	2	4
1,1,3,05	560092	4894900	I	679.7	11	S	8	4
1,1,3,06	560083	4894870	I	666.6	31	S	8	1
1,1,3,07	560074	4894840	I	642.5	31	S	2	4
1,1,3,08	560065	4894814	I	630.4	35	S	2	1
1,1,3,09	560057	4894784	I	618.7	22	SW	9	1
1,1,3,10	560048	4894755	I	604.8	35	W	9	1
1,1,3,11	560038	4894729	I	572.3	35	S	8	1
1,1,3,12	560029	4894699	I	563.5	35	S	8	6
1,1,3,13	560021	4894671	I	576.6	35	N	7	5
1,1,3,14	560013	4894643	I	601.7	33	NE	7	6

TABLE 11 (Continued)

Watershed, unit, transect, plot	Easting (UTM)	Northing (UTM)	GPS location[§]	Elevation (m)	Slope (°)	Aspect	Soil type[†]	Plant comm.[‡]
Watershed 1								
1,1,3,15	560008	4894612	M	619.5	35	N	7	6
1,1,3,16	559997	4894582	M	640.9	39	NE	1	5
1,1,3,17	559986	4894557	M	657.1	35	NE	1	2
1,1,3,18	559976	4894525	M	674.0	27	NE	1	2
1,1,3,19	559965	4894492	M	696.0	27	E	7	6
1,1,3,20	559960	4894469	M	699.3	19	NE	7	6
1,1,3,21	559950	4894435	M	710.1	22	E	7	6
1,1,3,22	559928	4894415	M	726.8	37	NE	1	6
1,1,3,23	559930	4894384	M	736.7	37	N	1	6
1,1,3,24	559920	4894356	M	751.3	19	N	1	2
1,1,4,01	560243	4894174	M	826.1	31	N	2	4
1,1,4,02	560256	4894196	M	818.1	29	N	2	4
1,1,4,03	560261	4894235	M	788.9	6	N	8	7
1,1,4,04	560265	4894258	M	772.4	39	N	8	6
1,1,4,05	560273	4894287	M	739.7	35	N	8	6
1,1,4,06	560282	4894315	M	716.3	11	NW	9	6
1,1,4,07	560294	4894350	M	703.2	17	N	7	5
1,1,4,08	560302	4894379	I	695.3	31	W	8	4
1,1,4,09	560311	4894406	I	712.6	31	SW	8	5
1,1,4,10	560318	4894435	I	727.1	35	W	8	5
1,1,4,11	560330	4894467	I	740.8	31	SW	8	2
1,1,4,12	560339	4894494	I	732.1	35	N	2	2
1,1,4,13	560349	4894523	I	711.3	35	N	2	5
1,1,4,14	560356	4894552	I	688.3	29	NW	2	6
1,1,4,15	560363	4894577	I	678.6	39	W	2	6
1,1,4,16	560373	4894606	I	673.6	35	W	9	6
1,1,4,17	560383	4894637	I	702.7	39	S	9	1
1,1,4,18	560391	4894666	I	728.0	42	S	7	7
1,1,4,19	560401	4894694	I	750.9	27	SW	7	4
1,1,4,20	560409	4894722	I	776.4	31	W	1	2
1,1,4,21	560418	4894751	I	795.0	17	E	2	1
1,1,4,22	560427	4894779	I	805.8	14	SE	2	1
1,1,4,23	560437	4894808	I	811.5	14	SE	1	4
1,1,4,24	560446	4894837	I	819.4	19	S	1	3
1,1,4,25	560454	4894864	I	829.7	31	S	1	3
1,1,4,26	560463	4894893	I	853.7	27	S	1	4
1,1,4,27	560473	4894922	I	871.2	29	SW	2	3
1,1,5,01	560721	4894826	M	886.7	3	S	5	2
1,1,5,02	560710	4894796	I	878.0	6	SW	3	2
1,1,5,03	560702	4894768	I	865.6	22	W	3	3
1,1,5,04	560694	4894739	I	852.9	27	W	3	5
1,1,5,05	560684	4894711	I	843.7	7	W	5	5
1,1,5,06	560676	4894683	I	836.9	3	W	5	4

TABLE 11 (Continued)

Watershed, unit, transect, plot	Easting (UTM)	Northing (UTM)	GPS location[§]	Elevation (m)	Slope (°)	Aspect	Soil type[†]	Plant comm.[‡]
Watershed 1								
1,1,5,07	560666	4894654	I	833.4	9	S	2	5
1,1,5,08	560657	4894627	I	835.5	31	N	2	5
1,1,5,09	560648	4894596	I	847.8	27	N	2	4
1,1,5,10	560639	4894566	I	851.5	24	W	2	4
1,1,5,11	560629	4894538	I	844.8	27	SW	2	4
1,1,5,12	560619	4894511	I	839.3	22	NW	8	4
1,1,5,13	560612	4894482	I	835.5	27	W	1	4
1,1,5,14	560602	4894453	I	852.2	35	N	2	4
1,1,5,15	560594	4894424	I	865.9	35	N	2	4
1,1,5,16	560584	4894395	I	869.8	24	SW	1	5
1,1,5,17	560577	4894368	I	868.9	33	SW	1	4
1,1,5,18	560567	4894341	I	860.5	27	W	1	4
1,1,5,19	560558	4894311	I	853.5	27	W	9	4
1,1,5,20	560550	4894283	I	845.7	31	W	9	6
1,1,5,21	560541	4894253	I	844.2	27	W	9	6
1,1,5,22	560531	4894225	I	851.7	35	W	9	6
1,1,5,23	560522	4894195	I	859.3	39	W	9	6
1,1,5,24	560512	4894167	I	878.6	39	NW	9	6
1,1,5,25	560506	4894139	I	898.5	35	N	9	6
1,1,5,26	560495	4894110	I	919.7	39	N	9	4
1,1,5,27	560486	4894081	I	932.7	35	NW	8	5
1,1,6,01	560909	4894871	M	966.2	19	W	3	2
1,1,6,02	560909	4894834	M	956.2	37	W	3	4
1,1,6,03	560902	4894810	M	945.0	3	W	3	2
1,1,6,04	560904	4894778	M	940.5	6	SW	3	4
1,1,6,05	560897	4894748	M	934.9	9	SW	3	2
1,1,6,06	560894	4894718	M	924.9	6	SW	3	4
1,1,6,07	560892	4894688	M	919.0	6	SW	3	4
1,1,6,08	560885	4894661	M	913.5	3	SW	3	4
1,1,6,09	560880	4894631	M	907.2	9	SW	3	2
1,1,6,10	560860	4894610	M	900.5	3	SW	5	2
1,1,6,11	560835	4894590	M	893.1	6	SW	3	4
1,1,6,12	560822	4894571	M	890.6	6	SW	3	5
1,1,6,13	560791	4894556	M	885.0	3	W	3	2
1,1,6,14	560767	4894534	M	881.8	3	W	5	5
1,1,6,15	560745	4894514	M	878.9	6	NW	5	2
1,1,6,16	560735	4894483	M	875.7	0	–	5	5
1,1,6,17	560727	4894452	M	873.6	6	SW	5	4
1,1,6,18	560719	4894420	M	872.4	0	–	5	5
1,1,6,19	560706	4894397	M	873.4	3	N	5	5
1,1,6,20	560695	4894368	M	877.0	9	NE	5	5
1,1,6,21	560688	4894337	M	880.0	9	N	2	4
1,1,6,22	560677	4894310	M	883.6	11	N	2	5

TABLE 11 (Continued)

Watershed, unit, transect, plot	Easting (UTM)	Northing (UTM)	GPS location§	Elevation (m)	Slope (°)	Aspect	Soil type†	Plant comm.‡
Watershed 1								
1,1,6,23	560670	4894279	M	891.4	11	N	1	6
1,1,6,24	560658	4894251	M	899.7	22	N	2	4
1,1,6,25	560651	4894225	M	914.9	35	NW	2	4
1,1,6,26	560640	4894197	M	921.7	11	NW	9	2
Watershed 3								
3,1,1,01	560829	4896196	M	558.4	9	W	4	3
3,1,1,02	560804	4896187	M	540.2	6	W	1	3
3,1,1,03	560778	4896172	M	526.5	39	W	1	6
3,1,2,01	560821	4896097	I	537.2	31	N	1	6
3,1,2,02	560855	4896115	M	542.0	40	S	1	7
3,1,2,03	560878	4896120	M	556.0	22	SW	1	4
3,1,2,04	560904	4896126	M	567.7	11	W	1	5
3,1,2,07	560984	4896163	M	613.7	31	W	1	2
3,1,2,08	561011	4896176	M	628.7	27	W	1	2
3,1,2,09	561037	4896190	M	637.9	6	W	1	3
3,1,3,02	561068	4896118	M	641.5	17	NW	1	3
3,1,3,03	561037	4896107	I	628.4	22	W	1	3
3,1,3,04	561005	4896096	M	610.2	9	W	1	2
3,1,3,05	560957	4896073	M	585.4	24	S	1	3
3,1,3,06	560927	4896058	M	560.4	6	W	1	5
3,1,3,08	560877	4896040	M	548.5	37	NE	2	6
3,1,4,01	560948	4895965	I	573.0	19	N	2	6
3,1,4,02	560974	4895976	I	566.0	31	N	2	2
3,1,4,04	561033	4895999	M	596.8	27	SW	8	7
3,1,4,05	561058	4896012	I	617.2	39	S	8	3
3,1,4,06	561085	4896024	M	630.4	35	SW	8	3
3,2,1,01	561683	4895542	I	858.7	6	N	3	5
3,2,1,02	561658	4895560	M	858.2	9	E	3	2
3,2,1,03	561634	4895575	I	858.7	0	–	3	2
3,2,1,04	561610	4895591	I	854.5	29	NW	3	5
3,2,1,05	561584	4895609	I	838.8	42	N	3	5
3,2,1,06	561557	4895628	I	822.0	29	N	3	4
3,2,1,07	561527	4895629	I	817.9	14	N	3	5
3,2,2,01	561714	4895639	I	839.2	35	W	2	6
3,2,2,02	561684	4895645	I	828.1	22	N	3	5
3,2,2,03	561655	4895650	I	826.8	19	N	3	5
3,2,2,04	561624	4895655	I	819.9	27	N	3	7
3,2,2,05	561595	4895662	I	806.0	39	NW	2	6
3,2,2,06	561564	4895667	I	790.6	35	N	2	6
3,2,2,07	561534	4895672	I	781.0	35	N	3	6
3,2,2,08	561506	4895677	I	782.9	37	N	3	5
3,2,3,01	561733	4895727	I	839.6	24	N	2	2
3,2,3,02	561706	4895728	I	830.4	31	NW	8	4

TABLE 11 (Continued)

Watershed, unit, transect, plot	Easting (UTM)	Northing (UTM)	GPS location[§]	Eleva-tion (m)	Slope (°)	Aspect	Soil type[†]	Plant comm.[‡]
Watershed 3								
3,2,3,03	561678	4895728	I	815.7	27	NW	2	3
3,2,3,04	561646	4895727	I	801.2	3	S	2	4
3,2,3,05	561614	4895727	I	779.1	33	SW	2	2
3,2,4,01	561758	4895813	I	840.1	6	W	2	3
3,2,4,02	561727	4895813	I	829.2	9	NW	6	3
3,2,4,03	561695	4895814	I	815.8	0	–	6	2
3,2,4,04	561665	4895813	I	811.9	0	–	6	2
3,2,4,05	561633	4895813	I	807.4	3	W	6	2
3,2,4,06	561604	4895813	I	799.9	24	W	2	4
3,2,4,07	561574	4895813	I	783.2	31	W	2	4
3,3,1,01	561092	4895483	M	810.6	35	N	2	4
3,3,1,02	561124	4895480	M	812.4	27	NE	2	5
3,3,1,03	561153	4895481	M	804.0	19	NE	2	6
3,3,1,04	561190	4895481	M	791.6	11	N	2	6
3,3,1,05	561214	4895481	I	794.5	3	N	8	7
3,3,1,06	561241	4895486	M	798.7	31	N	2	4
3,3,2,01	561149	4895386	M	839.4	6	N	2	5
3,3,2,02	561181	4895385	M	837.7	17	N	9	6
3,3,2,03	561209	4895385	M	837.3	9	N	8	4
3,3,2,04	561238	4895401	I	833.4	9	N	8	7
3,3,2,05	561265	4895413	M	830.1	9	N	8	5
3,3,2,06	561291	4895427	M	829.0	35	N	8	4
3,3,2,07	561318	4895440	I	829.6	33	N	8	7

[§] M = measured, I = interpolated.

[†] Soil type: 1 = Frissell, 2 = Limberlost, 3 = Andesite colluvium, 4 = McKenzie River, 5 = Budworm, 6 = Slipout, 7 = Stony Frissell, 8 = Stony Limberlost, 9 = Talus (see Rothacher et al. 1967).

[‡] Plant community: 1 = *Corylus cornuta - Gaultheria shallon*, 2 = *Rhododendron macrophyllum - Gaultheria shallon*, 3 = *Acer circinatum - Gaultheria shallon*, 4 = *Acer circinatum - Berberis nervosa,* 5 = *Coptis laciniata*, 6 = *Polystichum munitum*, 7 = Unclassified (see Rothacher et al. 1967).

Vendor contact information for GIS software and data as of January 1, 2005:
OBEC Consulting Engineers, 920 Country Club Road, Suite 100B, Eugene, OR 97401-2208. Telephone: 1-541-683-6090, http://www.obec.com

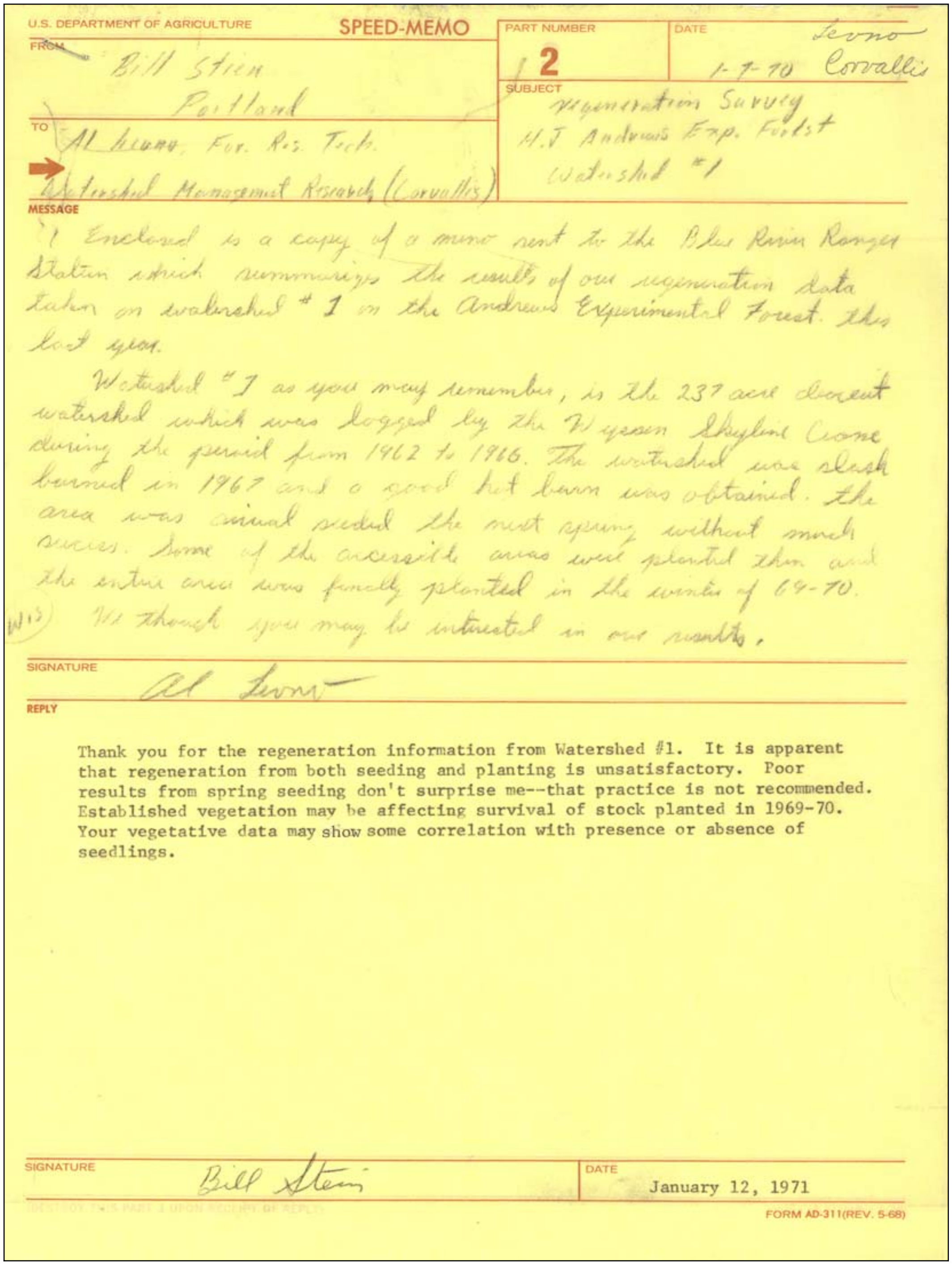
Trimble Navigation Limited, 749 North Mary Ave, Sunnyvale, CA 94085. Telephone: 1-408-481-8000, http://www.trimble.com

ESRI, 380 New York Street, Redlands, CA 92373-8100. Telephone: 1-909-793-2853, http://www.ersi.com

OBEC Antenna Coordinates
Latitude: 44° 3' 57.45762" N
Longitude: 123° 5' 53.28105" W
Height: 112.235 m
Receiver Type: Trimble 4400
Elevation Mask: 10°

APPENDIX IV: HISTORICAL MANAGEMENT DOCUMENTS

Historical documents were consulted to understand the potential contributions of seeding and planting of *Pseudotsuga* to stand development. The tree densities reported in these memos suggest that the majority of *Pseudotsuga* stems regenerated naturally. The first memo, written in 1970 (Fig. 14), describes the generally poor regeneration that followed the first aerial seeding of WS1. The next memo, written in 1971 by Al Levno of the USDA Forest Sciences Laboratory in Corvallis, OR (Fig. 15, map Fig. 16), indicates that natural regeneration had improved considerably over earlier years, but planted *Pseudotsuga* showed poor survivorship between 1969 and 1970. The memo written in 1971 by Floyd Damoth of the USDA Blue River Ranger District, Willamette National Forest, Blue River, OR (Fig. 17, map Fig. 18), confirms the levels of natural regeneration. It also outlines plans for some limited replanting of a portion of WS1. Since planting activities were managed by the Blue River Ranger District, the unstocked and partially stocked areas in Fig. 18 were probably the only areas replanted. However, stand data were the responsibility of the Forest Science Laboratory, and the area replanted noted in the text refers to the larger unstocked and partially stocked area in Fig. 16. The final memo is a summary of stocking levels in 1973, two years after the last management activities were undertaken.



U.S. DEPARTMENT OF AGRICULTURE

SPEED-MEMO

PART NUMBER 2

DATE 1-7-70

Levno
Corvallis

FROM Bill Stein
Portland

TO Al Levno, For. Res. Tech.
Watershed Management Research (Corvallis)

SUBJECT regeneration Survey
H.J Andrews Exp. Forest
Watershed #1

MESSAGE

Enclosed is a copy of a memo sent to the Blue River Ranger Station which summarizes the results of our regeneration data taken on watershed #1 in the Andrews Experimental Forest this last year.

Watershed #1 as you may remember, is the 237 acre clearcut watershed which was logged by the Wyssen Skyline Crane during the period from 1962 to 1966. The watershed was slash burned in 1967 and a good hot burn was obtained. the area was aerial seeded the next spring without much success. Some of the accessible areas were planted then and the entire area was finally planted in the winter of 69-70.

W13

We thought you may be interested in our results.

SIGNATURE Al Levno

REPLY

Thank you for the regeneration information from Watershed #1. It is apparent that regeneration from both seeding and planting is unsatisfactory. Poor results from spring seeding don't surprise me--that practice is not recommended. Established vegetation may be affecting survival of stock planted in 1969-70. Your vegetative data may show some correlation with presence or absence of seedlings.

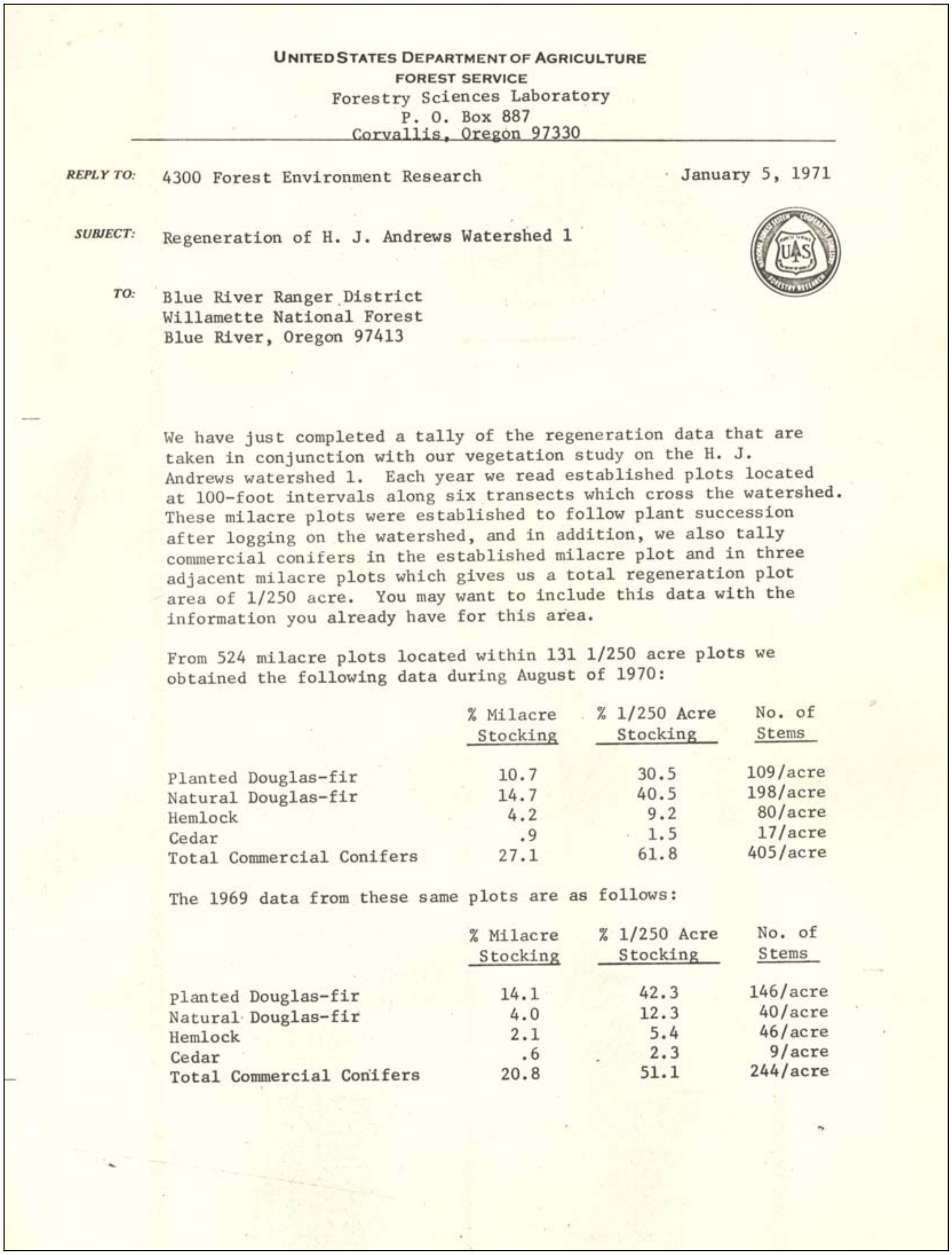
SIGNATURE Bill Stein

DATE January 12, 1971

DESTROY THIS PART 1 UPON RECEIPT OF REPLY

FORM AD-311(REV. 5-68)

FIG. 14. Management memo, January 7, 1970.



UNITED STATES DEPARTMENT OF AGRICULTURE
FOREST SERVICE
Forestry Sciences Laboratory
P. O. Box 887
Corvallis, Oregon 97330

REPLY TO: 4300 Forest Environment Research

January 5, 1971

SUBJECT: Regeneration of H. J. Andrews Watershed 1

TO: Blue River Ranger District
Willamette National Forest
Blue River, Oregon 97413

We have just completed a tally of the regeneration data that are taken in conjunction with our vegetation study on the H. J. Andrews watershed 1. Each year we read established plots located at 100-foot intervals along six transects which cross the watershed. These milacre plots were established to follow plant succession after logging on the watershed, and in addition, we also tally commercial conifers in the established milacre plot and in three adjacent milacre plots which gives us a total regeneration plot area of 1/250 acre. You may want to include this data with the information you already have for this area.

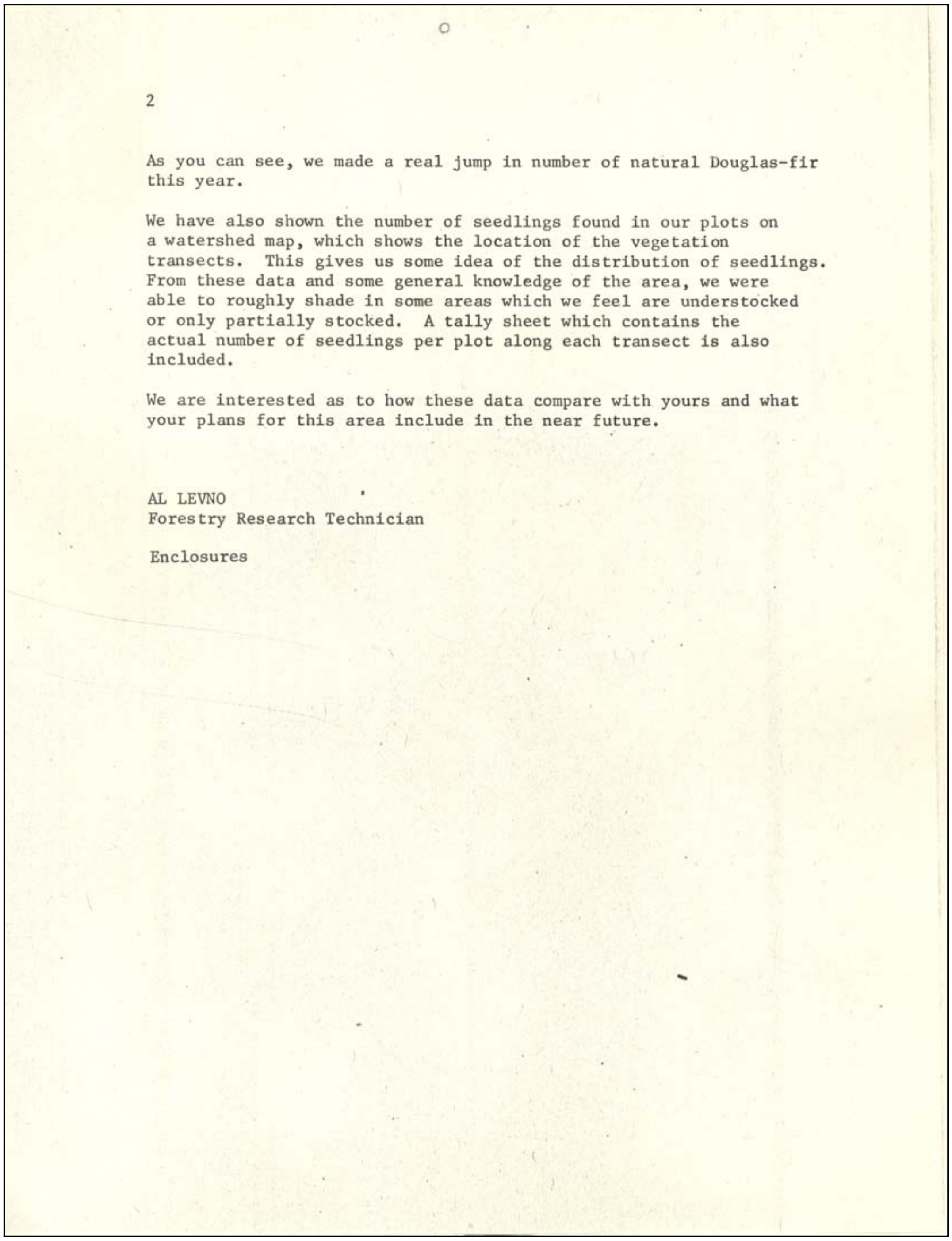
From 524 milacre plots located within 131 1/250 acre plots we obtained the following data during August of 1970:

	% Milacre Stocking	% 1/250 Acre Stocking	No. of Stems
Planted Douglas-fir	10.7	30.5	109/acre
Natural Douglas-fir	14.7	40.5	198/acre
Hemlock	4.2	9.2	80/acre
Cedar	.9	1.5	17/acre
Total Commercial Conifers	27.1	61.8	405/acre

The 1969 data from these same plots are as follows:

	% Milacre Stocking	% 1/250 Acre Stocking	No. of Stems
Planted Douglas-fir	14.1	42.3	146/acre
Natural Douglas-fir	4.0	12.3	40/acre
Hemlock	2.1	5.4	46/acre
Cedar	.6	2.3	9/acre
Total Commercial Conifers	20.8	51.1	244/acre

FIG. 15A. Management memo, January 5, 1971 (Page 1).



2

As you can see, we made a real jump in number of natural Douglas-fir this year.

We have also shown the number of seedlings found in our plots on a watershed map, which shows the location of the vegetation transects. This gives us some idea of the distribution of seedlings. From these data and some general knowledge of the area, we were able to roughly shade in some areas which we feel are understocked or only partially stocked. A tally sheet which contains the actual number of seedlings per plot along each transect is also included.

We are interested as to how these data compare with yours and what your plans for this area include in the near future.

AL LEVNO
Forestry Research Technician

Enclosures

FIG. 15B. Management memo, January 5, 1971 (Page 2).

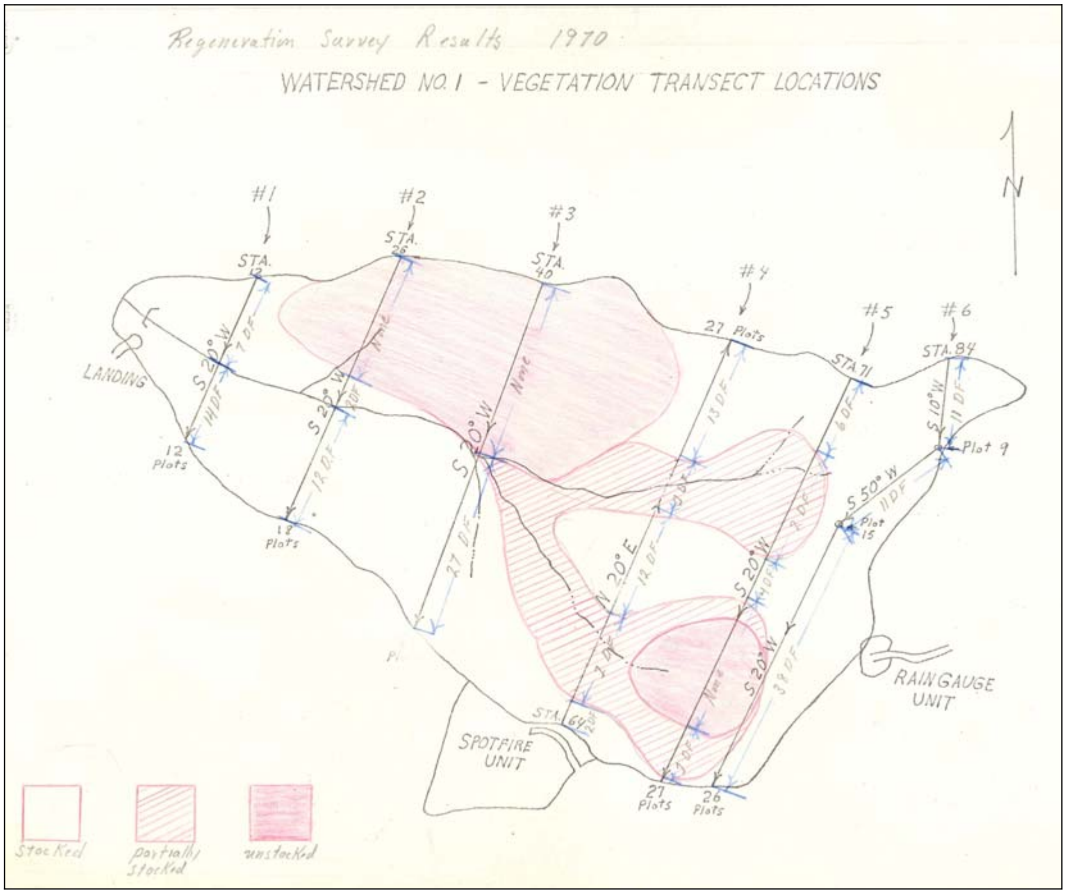
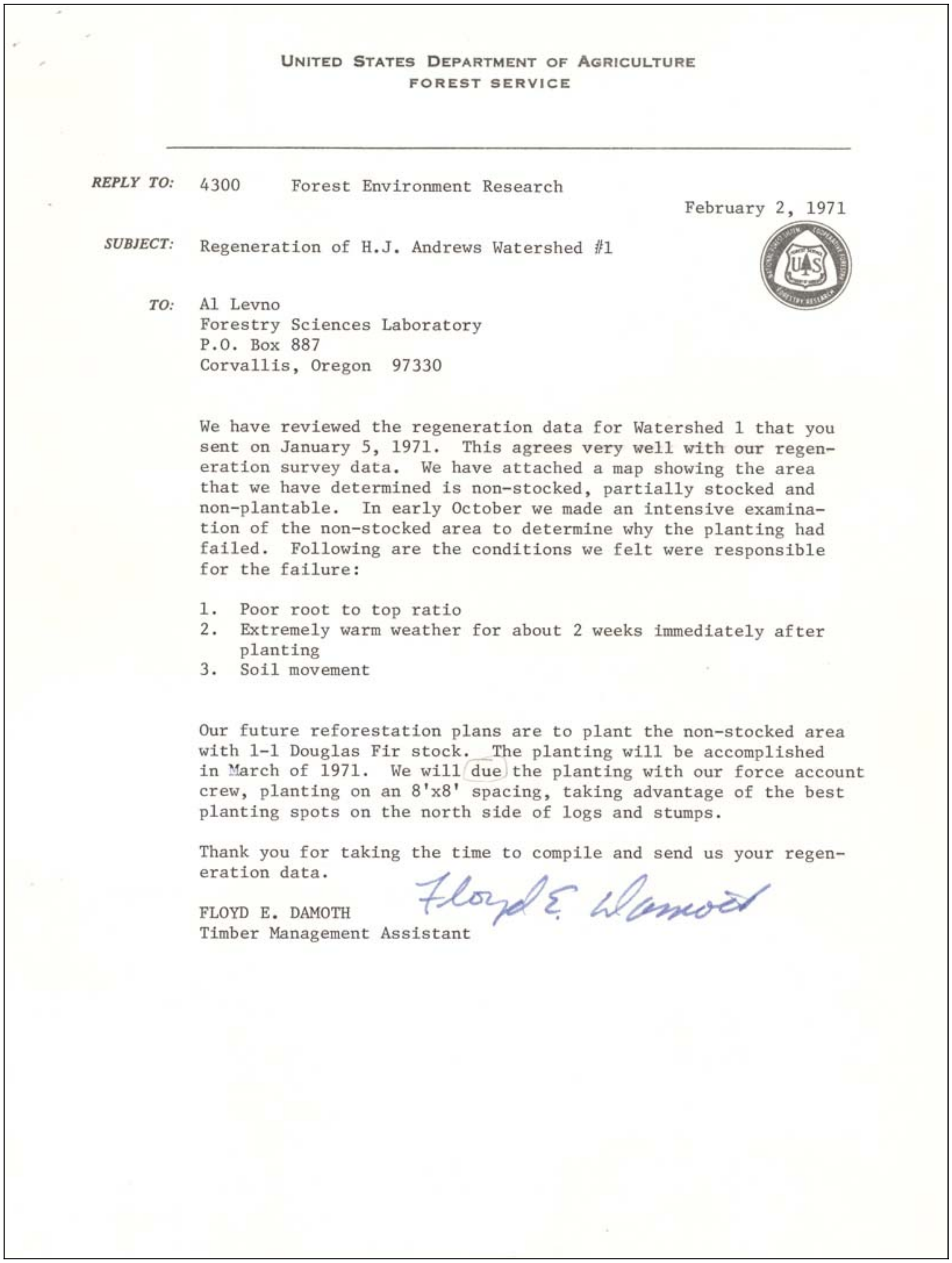


FIG. 16. Map of regeneration survey results in 1970 (USDA Forest Service, Forest Sciences Laboratory, Corvallis, OR 97330).



UNITED STATES DEPARTMENT OF AGRICULTURE
FOREST SERVICE

REPLY TO: 4300 Forest Environment Research

February 2, 1971

SUBJECT: Regeneration of H.J. Andrews Watershed #1

TO:
Al Levno
Forestry Sciences Laboratory
P.O. Box 887
Corvallis, Oregon 97330

We have reviewed the regeneration data for Watershed 1 that you sent on January 5, 1971. This agrees very well with our regeneration survey data. We have attached a map showing the area that we have determined is non-stocked, partially stocked and non-plantable. In early October we made an intensive examination of the non-stocked area to determine why the planting had failed. Following are the conditions we felt were responsible for the failure:

1. Poor root to top ratio
2. Extremely warm weather for about 2 weeks immediately after planting
3. Soil movement

Our future reforestation plans are to plant the non-stocked area with 1-1 Douglas Fir stock. The planting will be accomplished in March of 1971. We will due the planting with our force account crew, planting on an 8'x8' spacing, taking advantage of the best planting spots on the north side of logs and stumps.

Thank you for taking the time to compile and send us your regeneration data.

Floyd E. Damoth

FLOYD E. DAMOTH
Timber Management Assistant

FIG. 17. Management memo, February 2, 1971.

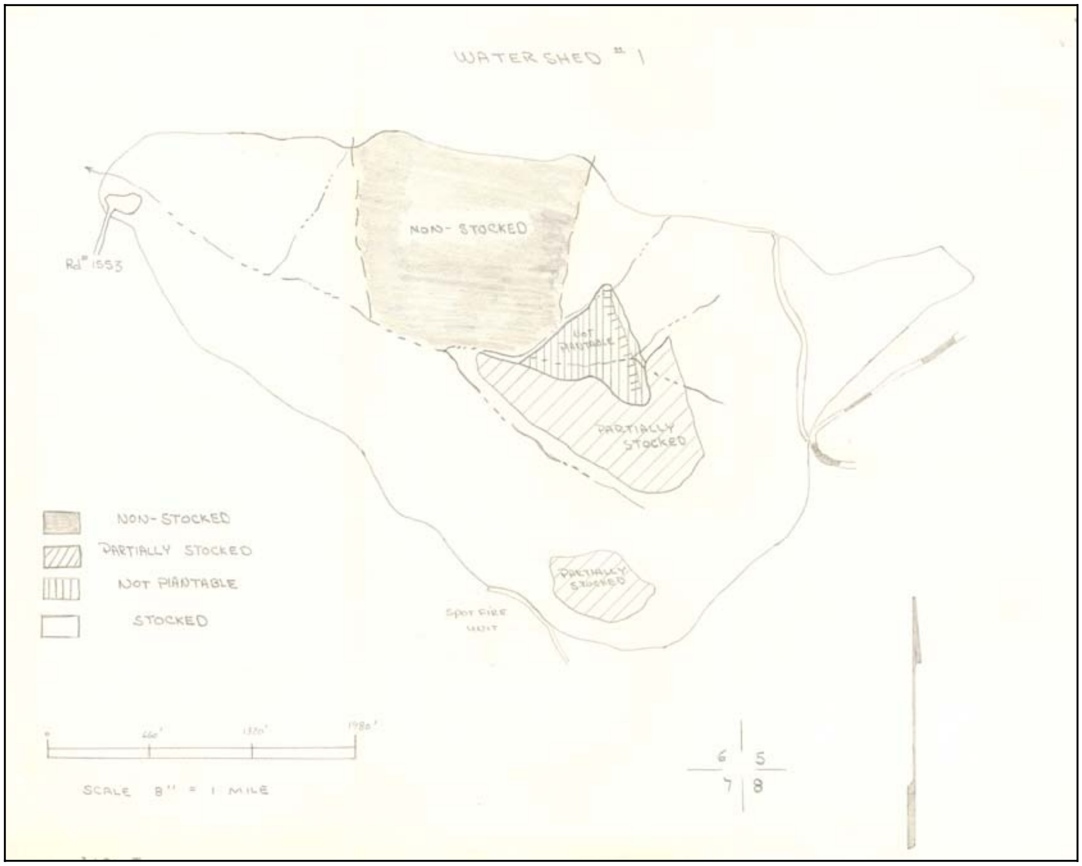
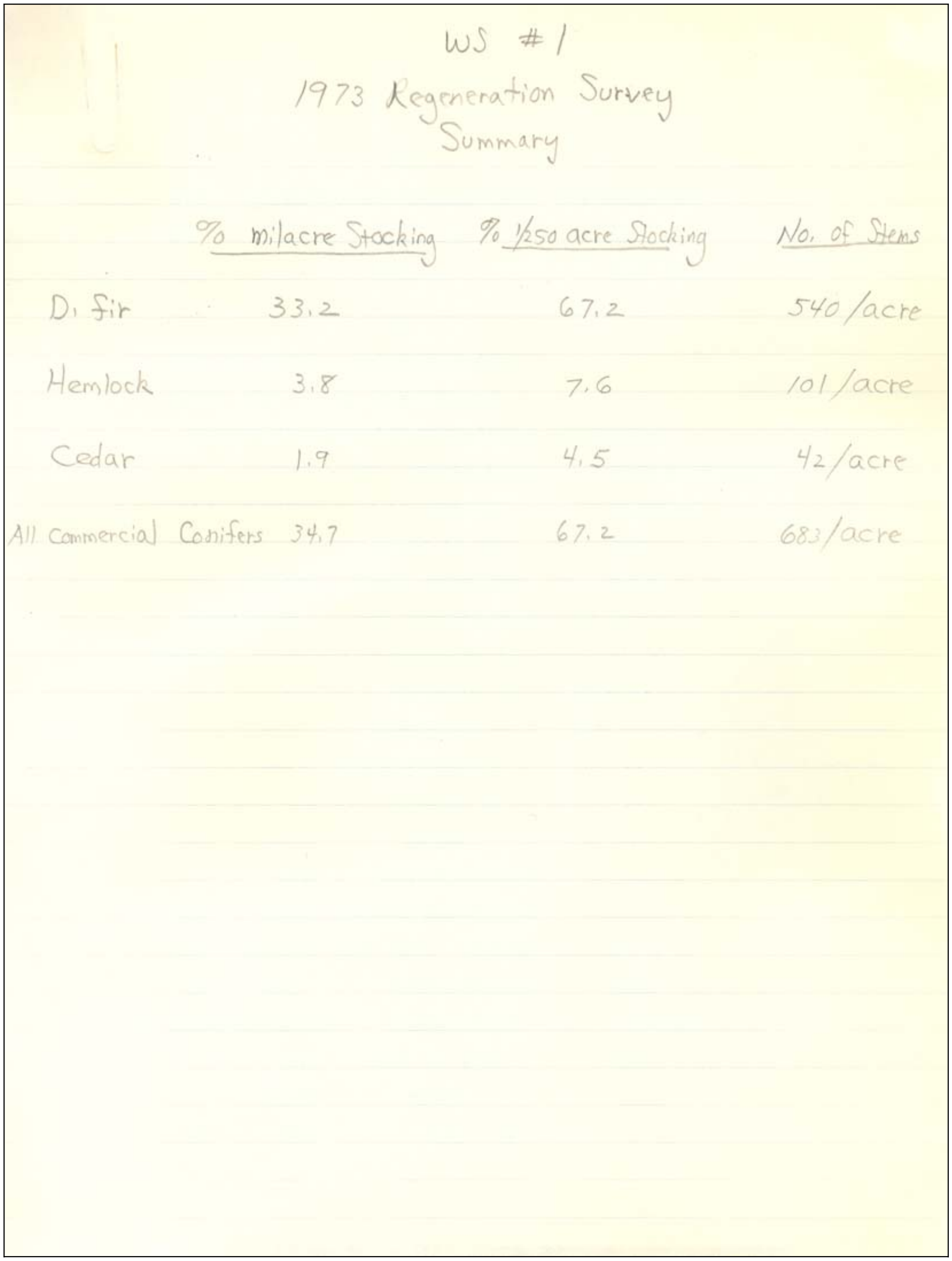


FIG. 18. Map of regeneration survey results in 1970 (USDA Forest Service, Blue River Ranger District, Willamette National Forest, Blue River, OR 97413).



WS #1
1973 Regeneration Survey
Summary

	% milacre Stocking	% 1/250 acre Stocking	No. of Stems
D. fir	33.2	67.2	540/acre
Hemlock	3.8	7.6	101/acre
Cedar	1.9	4.5	42/acre
All Commercial Conifers	34.7	67.2	683/acre

FIG. 19. Unattributed notes from the last regeneration survey in 1973 (USDA Forest Service files, Forest Sciences Laboratory, Corvallis, OR 97330).

APPENDIX V: PHOTOGRAPHIC RECORDS OF DISTURBANCE

Photographic evidence of changes in vegetation has been collected since study initiation. Older photographs are part of the HJ Andrews archives and the photographer is attributed when known. All other photographs are by the author.

FIG. 20. Aerial photo of WS1 prior to harvest (1959, left) and 1 yr after broadcast burning (1967, right).

FIG. 21. Gradual revegetation of north-facing slope of WS1 from 1967 to 1988 (left photo Al Levno, right photo Charles B. Halpern).

FIG. 22. Coexistence of *Pseudotsuga, Tsuga, Thuja, Arbutus* and *Castanopsis* in young forest (left, 35 yr after disturbance) and *Pseudotsuga, Tsuga, Arbutus*, *Castanopsis* and *Pinus lambertiana* in old growth (right, c. 500 yr old).

FIG. 23. Old-growth crushing mortality (left, 1987, looking downslope) and (right, 2004, looking upslope). This old-growth *Pseudotsuga* snapped at the base due to *Phaeolus schweinitzii* infection. Left photo Charles B. Halpern.

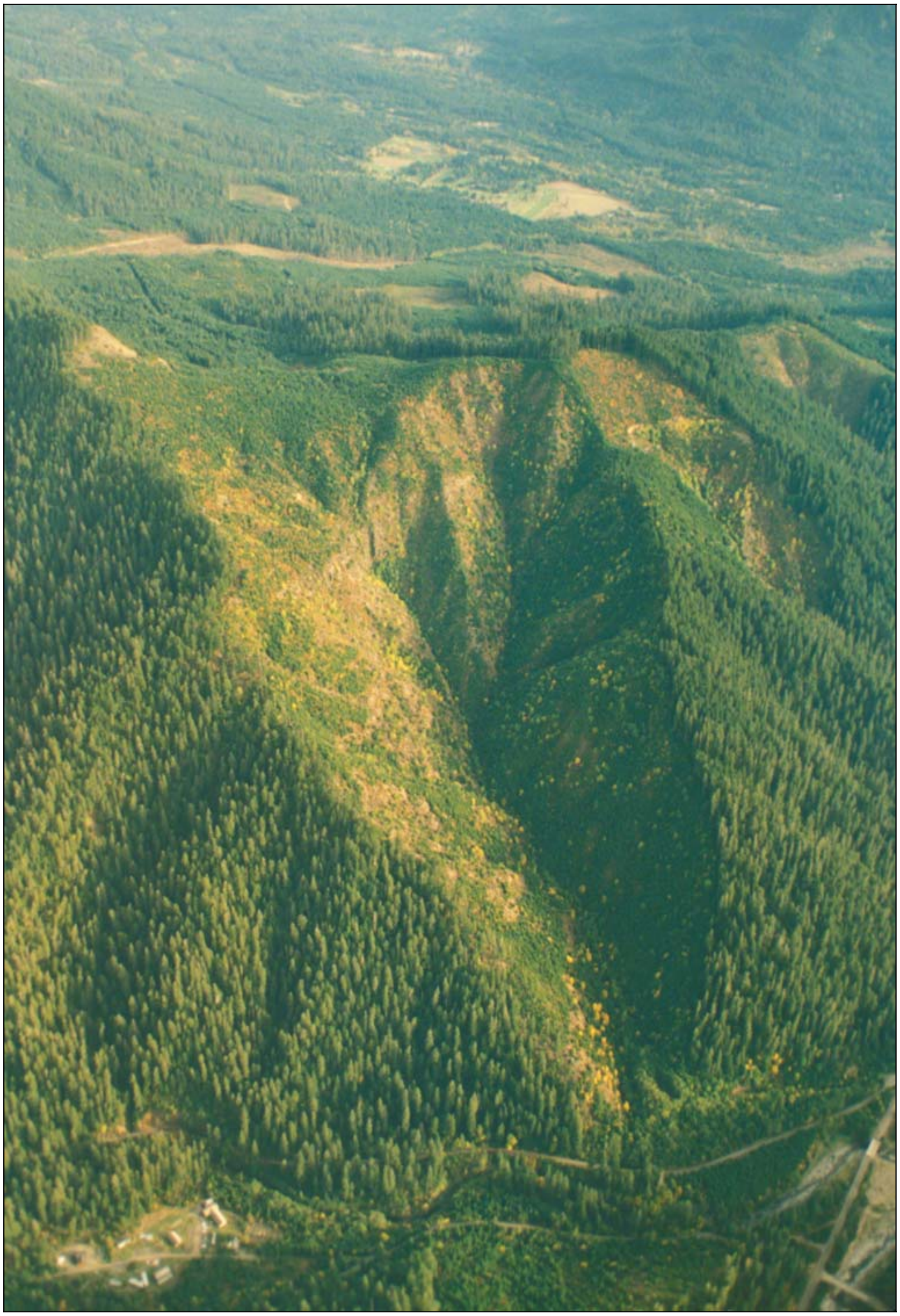


FIG. 24. Aerial photo of WS1 showing abundant clumps of *Acer macrophyllum* (1988). Photo Al Levno

FIG. 25. A thick patch of *Acer circinatum* with *Pseudotsuga* visible in the background (WS1, S ridge).

FIG. 26. A remnant stump with regenerating *Pseudotsuga* of various size classes in the background. Understory vegetation includes *Rhododendron macrophyllum, Berberis nervosa, Acer circinatum, Pteridium aquilinum* and *Polystichum munitum*. Note snapped *Pseudotsuga* at right (top of WS1).

FIG. 27. Vigorous *Pseudotsuga* on south-facing slope in WS3. Understory includes *Rhododendron macrophyllum, Gaultheria shallon*, and *Berberis nervosa*.

FIG. 28. North and south aspects in WS3, Unit 1 illustrating the range of soil and vegetation. Closed canopy *Pseudotsuga* and *Tsuga* (right) meet shallow exposed soils (left) that do not yet support trees.

FIG. 29. Mechanical mortality creates a gap in WS3, Unit 3 (2004).

FIG. 30. A plot in WS3 dominated by shade-tolerant species (mostly *Tsuga heterophylla*) from 1979 – 2001. *Polystichum munitum* and moss form a depauperate understory.

FIG. 31. A *Tsuga* stem that survived crushing and continues to grow recumbent. Branches have reoriented and bear fresh cones (WS3, Unit 3, 2004).

FIG. 32. A large gap created by mechanical mortality. Many stems are snapped, and boles and branches cover the forest floor. Tip-up mounds in this gap are 1 – 2 m in diameter (WS1, 2004).

APPENDIX VI: CODE IMPLEMENTATION

Visual Basic code for DBH calculations

After developing the regression equations to relate diameter at the base to dbh, the code was implemented in Visual Basic using base worksheets in Excel.

```
' assumes there are five ranges declared:  Species, Watershed, DBA, DBH,
CalculatedDBH
' Species is a string value
' Watershed is a double value
' DBA is a double value
' DBH is a double value
' CalculatedDBH is the result of the macro - double

Sub subCalculate_DBA_From_DBH()
    Dim i As Integer

    i = 1

    Do Until Range("Species").Cells(i).Value = ""
        Range("CalculatedDBH").Cells(i).Value =
fncDBH(Range("Species").Cells(i).Value, Range("Watershed").Cells(i),
Range("DBA").Cells(i).Value, Range("DBH").Cells(i).Value)
        i = i + 1
    Loop
End Sub


Function fncDBH(Species As String, Watershed As Double, DBA As Double, DBH As
Double)

    If DBA = 0 Then
        fncDBH = 0
        ' This is the case when we do not have a value we want to interpolate.
    ElseIf DBH <> 0 Then
        fncDBH = 0
        ' This is the case for our predictors - we do not want to overwrite the
actual values.
    Else

        If Species = "ABAM" Then
            fncDBH = fncPSME(Watershed, DBA)
            ' The proxy for ABAM is PSME, based on morphology. Use same watershed.
        ElseIf Species = "ACMA" Then
            fncDBH = fncACMA(DBA)
        ElseIf Species = "ALRU" Then
            fncDBH = fncALRU(DBA)
        ElseIf Species = "ARME" Then
            fncDBH = fncARME(DBA)
        ElseIf Species = "CACH" Then
            fncDBH = fncCACH(DBA)
        ElseIf Species = "CONU" Then
            fncDBH = fncCONU(DBA)
        ElseIf Species = "LIDE2" Then
            fncDBH = fncTHPL(DBA)
            ' The proxy for LIDE2 is THPL.
        ElseIf Species = "POTR2" Then
            fncDBH = fncALRU(DBA)
            ' The proxy for POTR2 is ALRU.
        ElseIf Species = "PREM" Then
            fncDBH = fncPREM(DBA)
        ElseIf Species = "PSME" Then
            fncDBH = fncPSME(Watershed, DBA)
        ElseIf Species = "RHPU" Then
            fncDBH = fncCONU(DBA)
            ' The proxy for RHPU is CONU.
        ElseIf Species = "TABR" Then
            fncDBH = fncTABR(DBA)
```

```
        ElseIf Species = "THPL" Then
            fncDBH = fncTHPL(DBA)
        ElseIf Species = "TSHE" Then
            fncDBH = fncTSHE(DBA)

    Else
        fncDBH = -1
        ' In this case there has been an unknown species.

    End If
    End If

End Function

Function fncACMA(DBA As Double) As Double
    fncACMA = 0.587 * DBA + 0.398
End Function

Function fncALRU(DBA As Double) As Double
    fncALRU = 0.647 * DBA + 0.631
End Function

Function fncARME(DBA As Double) As Double
    fncARME = 0.389 * DBA + 1.428
End Function

Public Function fncCACH(DBA As Double) As Double
    fncCACH = 0.736 * DBA - 0.373
End Function

Function fncCONU(DBA As Double) As Double
    fncCONU = 0.686 * DBA + 0.034
End Function


Function fncPREM(DBA As Double) As Double
    fncPREM = 0.654 * DBA + 0.228
End Function

Function fncPSME(Watershed As Double, DBA As Double) As Double
    If Watershed = 1 Then
        fncPSME = 0.618 * DBA + 0.402
    ElseIf Watershed = 3 Then
        fncPSME = 0.832 * DBA - 0.574
    Else
        fncPSME = -1
    End If
End Function

Function fncTABR(DBA As Double) As Double
    fncTABR = 0.677 * DBA - 0.051
End Function

Function fncTHPL(DBA As Double) As Double
    fncTHPL = 0.665 * DBA - 0.07
End Function

Function fncTSHE(DBA As Double) As Double
    fncTSHE = 0.723 * DBA - 0.091
End Function
```

Visual Basic code for biomass calculations

After receiving the methodology from Acker 2002, biomass was calculated from DBH using code implemented in Visual Basic.

```
' Assumes there are three ranges declared:  Species, FinalDBH, Biomass
' Species is a string value
' DBH is a double value
' Biomass is the result of the macro - double
```

```
Sub subCalculate_Biomass_From_DBH()
    Dim i As Integer

    i = 1

    Do Until Range("Species").Cells(i).Value = "END_OF_DATA"
        Range("Biomass").Cells(i).Value =
fncBiomass(Range("Species").Cells(i).Value, Range("FinalDBH").Cells(i).Value)
        i = i + 1
    Loop
End Sub


Function fncBiomass(Species As String, DBH As Double)

    If DBH = 0 Then
        fncBiomass = ""
        'This is the case when we do not have any value.
    Else
        If Species = "ABAM" Then
            fncBiomass = fncBiomassPSME(DBH)
            ' The proxy for ABAM is PSME.
        ElseIf Species = "ACMA" Then
            fncBiomass = fncBiomassACMA(DBH)
        ElseIf Species = "ALRU" Then
            fncBiomass = fncBiomassALRU(DBH)
        ElseIf Species = "ARME" Then
            fncBiomass = fncBiomassARME(DBH)
        ElseIf Species = "CACH" Then
            fncBiomass = fncBiomassCACH(DBH)
        ElseIf Species = "CONU" Then
            fncBiomass = fncBiomassALRU(DBH)
            ' The proxy for CONU is ALRU.
        ElseIf Species = "LIDE2" Then
            fncBiomass = fncBiomassTHPL(DBH)
            ' The proxy for LIDE2 is THPL.
        ElseIf Species = "POTR2" Then
            fncBiomass = fncBiomassALRU(DBH)
            ' The proxy for POTR2 is ALRU.
        ElseIf Species = "PREM" Then
            fncBiomass = fncBiomassALRU(DBH)
            ' The proxy for PREM is ALRU.
        ElseIf Species = "PSME" Then
            fncBiomass = fncBiomassPSME(DBH)
        ElseIf Species = "RHPU" Then
            fncBiomass = fncBiomassALRU(DBH)
            ' The proxy for RHPU is ALRU.
        ElseIf Species = "TABR" Then
            fncBiomass = fncBiomassTABR(DBH)
        ElseIf Species = "THPL" Then
            fncBiomass = fncBiomassTHPL(DBH)
        ElseIf Species = "TSHE" Then
            fncBiomass = fncBiomassTSHE(DBH)
        ElseIf Specie = "" Then
            fncBiomass = ""
            'This allows for the case of blank lines, so plot summary sheets are
accomodated.
    Else
        fncBiomass = -1
        'In this case there has been an unknown species.

    End If
    End If

End Function

Function fncBiomassACMA(DBH As Double) As Double
    Dim Height As Double
    Dim Volume As Double

    'Height was computed from DBH using equations from Garman et al. 1995.  The
form of the height equation is
    'HT = 1.37 + (b0*(1-exp(b1*DBH))^b2).
    'ACMA     N OR Cascades  30.41311     -0.034245     0.682100
```

```
    Height = 1.37 + (30.41311 * (1 - Exp(-0.034245 * DBH)) ^ 0.6821)

    'Volume = b0*(DBH^b1)*(HT^b2)
    'SPECIES   BIOPAK_NO  B0             B1         B2
    'ACMA      654        0.0000718042   2.224620   0.575610

   Volume = 0.0000718042 * (DBH ^ 2.22462) * (Height ^ 0.57561)

   'Density values provided by Mark Harmon

    fncBiomassACMA = Volume * 0.44
End Function

Function fncBiomassALRU(DBH As Double) As Double
    fncBiomassALRU = Exp(3.97 + (2.56 * Log(DBH))) 'Result in grams
    fncBiomassALRU = fncBiomassALRU / 1000000 'Divide by 1,000,000 for Mg

    'BIOPAK Equation Number 266
    'Biomass = exp(b0+b1*ln(DBH)) [result in g, divide by 1e6 for Mg]
    'SPECIES   BIOPAK_NO  B0             B1
    'ALRU      266        3.97           2.56
End Function

Function fncBiomassARME(DBH As Double) As Double
    Dim Height As Double
    Dim Volume As Double

    'Height was computed from DBH using equations from Garman et al. 1995.  The
form of the height equation is
    'HT = 1.37 + (b0*(1-exp(b1*DBH))^b2).
    'ARME     S OR Cascades  24.212490    -0.033914     0.891708

    Height = 1.37 + (24.21249 * (1 - Exp(-0.033914 * DBH)) ^ 0.891708)

    'Volume = b0*(DBH^b1)*(HT^b2)
    'SPECIES   BIOPAK_NO  B0             B1         B2
    'ARME      674        0.0000378129   1.992950   1.015320

    Volume = 0.0000378129 * (DBH ^ 1.99295) * (Height ^ 0.891708)

    'Density values provided by Mark Harmon

    fncBiomassARME = Volume * 0.56
End Function

Public Function fncBiomassCACH(DBH As Double) As Double
    Dim Height As Double
    Dim Volume As Double

    'Height was computed from DBH using equations from Garman et al. 1995.  The
form of the height equation is
    'HT = 1.37 + (b0*(1-exp(b1*DBH))^b2).
    'CACH     N OR Coastal   40.664790    -0.017775     0.873626

    Height = 1.37 + (40.66479 * (1 - Exp(-0.017775 * DBH)) ^ 0.873626)

    'Volume = b0*(DBH^b1)*(HT^b2)
    'SPECIES   BIOPAK_NO  B0             B1         B2
    'CACH      663        0.0001169607   2.022320   0.686380

    Volume = 0.0001169607 * (DBH ^ 2.02232) * (Height ^ 0.68638)

    'Density values provided by Mark Harmon

    fncBiomassCACH = Volume * 0.42
End Function

Function fncBiomassPSME(DBH As Double) As Double
    Dim BarkVolume As Double
    Dim WoodVolume As Double

    'The resulting volume equations were of the form Vol = b0*(DBH^b1).
    'SPECIES  N         B0        B1       R_SQ
    'PSME   611   0.0001123560  2.509359 0.9718

    WoodVolume = 0.000112356 * (DBH ^ 2.509359)
```

```
    BarkVolume = WoodVolume * 0.29

    'Wood and bark density values were obtained from the optical dendrometer
dataset (TV0098).
    'SPECIES                        COMP              DENSITY
    'PSME                           B                 0.438
    'PSME                           W                 0.452

    fncBiomassPSME = (BarkVolume * 0.438) + (WoodVolume * 0.452)
End Function

Function fncBiomassTABR(DBH As Double) As Double
    Dim BarkVolume As Double
    Dim WoodVolume As Double

    'This calculation uses TSHE as a proxy, except for wood density.
    'TABR bark density was taken to be the same as TSHE bark density.
    'TABR wood density was taken to be 0.60 (source: Mark Harmon).

     'The resulting volume equations were of the form Vol = b0*(DBH^b1).
    'SPECIES  N     B0            B1       R_SQ
    'TSHE   272   0.0003720880  2.259720 0.9536

    WoodVolume = 0.000372088 * (DBH ^ 2.25972)
    BarkVolume = WoodVolume * 0.124

    fncBiomassTABR = (BarkVolume * 0.415) + (WoodVolume * 0.6)
End Function

Function fncBiomassTHPL(DBH As Double) As Double
    Dim BarkVolume As Double
    Dim WoodVolume As Double

    'The resulting volume equations were of the form Vol = b0*(DBH^b1).
    'SPECIES  N     B0            B1       R_SQ
    'THPL    64   0.0003339420  2.197256 0.9478

    WoodVolume = 0.000333942 * (DBH ^ 2.197256)
    BarkVolume = WoodVolume * 0.082


    'Wood and bark density values were obtained from the optical dendrometer
dataset (TV0098).
    'SPECIES                        COMP              DENSITY
    'THPL                           B                 0.333
    'THPL                           W                 0.312

    fncBiomassTHPL = (BarkVolume * 0.333) + (WoodVolume * 0.312)
End Function

Function fncBiomassTSHE(DBH As Double) As Double
    Dim BarkVolume As Double
    Dim WoodVolume As Double

    'The resulting volume equations were of the form Vol = b0*(DBH^b1).
    'SPECIES  N     B0            B1       R_SQ
    'TSHE   272   0.0003720880  2.259720 0.9536

    WoodVolume = 0.000372088 * (DBH ^ 2.25972)
    BarkVolume = Volume * 0.124

    'Wood and bark density values were obtained from the optical dendrometer
dataset (TV0098).
    'SPECIES                        COMP              DENSITY
    'TSHE                           B                 0.415
    'TSHE                           W                 0.421

    fncBiomassTSHE = (BarkVolume * 0.415) + (WoodVolume * 0.421)
End Function
```